TESTING FOR EVIDENCE OF HIERARCHICAL SYSTEM STRUCTURE IN THE MANITOBAN BOREAL FOREST

By

PAUL C. MARPLES

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TESTING FOR EVIDENCE OF HIERARCHICAL SYSTEM STRUCTURE IN THE MANITOBAN BOREAL FOREST

By

Paul C. Marples

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Major Department: Zoology

A controversial extension of hierarchy theory has been proposed for ecology. It contends that over a given scale range, ecosystems are controlled by only a few, often biotic processes operating at distinct periodicities. Slowly cycling processes create large structure and rapidly cycling processes create small structure. Overall metrics of physical structure are thus predicted to fall into multimodal size distributions. The objective of this project was to partially evaluate the applicability of this theory to wildfire and mammals of the boreal forest.

First I tested whether stand age exerts a feedback control over fire and thereby constrains the distribution of fire sizes into multiple modes. Specifically, I tested whether burn hazard increased with stand age. Spatially explicit records of all fires occurring in Southeast Manitoba (1928-1990) were

analyzed. Regression analysis found that burn hazard does not increase with stand age.

Existing statistical methods cannot effectively detect real modes exclusively when complex multimodality is encountered. Therefore, I introduce Lump Simulation (LS) as a new statistical method. LS divides data aggregations over many resolutions (i.e., degrees of smoothing). Potential multimodality is indicated whenever the location of aggregations correlates amongst multiple data sets at a specific resolution. Such apparent matching is tested for significance through simulation.

The application of LS to mammal body mass of the Eastern North American, Northern European, and Eastern Russian boreal forests revealed 10-11 modes in these distributions. A separate application of LS found that the distribution of fire sizes (1976-1991) in the Manitoban boreal forest is not multimodal.

In summary, the application of this extension of hierarchy theory to boreal forest mammals is contingent upon further testing. Its application to wildfire in the Manitoban boreal forest is limited because the factors that control wildfire seem to be many in number and/or highly stochastic. These results have implications for the short-term effects of potential climate change. Any increase in fire occurrence should not be complicated by existing vegetation age structure and simply result in an upward displacement of the continuous fire-size distribution.

CHAPTER 1
INTRODUCTION AND OVERVIEW

The universe we live in is, at least to some degree, structured hierarchically. Strong and weak forces dominate within the nucleus, electrochemical forces dominate at the molecular level, and gravity dominates outside the biosphere. Thus, over discrete scale ranges, unique sets of forces interact strongly and in relative isolation. The question remains, however, to what degree ecological systems are structured hierarchically as Allen and Starr (1982) and O'Neill et al. (1986) suggest.

At present, ecology is at a crossroads as it wrestles with the assumptions inherent to old perspectives, while it considers new, general theories (Pickett et al. 1994). Two long-standing and opposing perspectives that have dominated the field of ecology were proposed by Clements (1916) and Gleason (1926). The Gleasonian view conservatively considered the distribution and abundance of all species to be largely a function of exploitation and/or tolerance of a diverse set of site-specific conditions. Conditions differ from site to site, so generality is lacking. Clements, however, argued that within broad abiotic constraints, ecosystems converge to a predictable, general, holistic structure through biotic regulation. While it is well recognized that biotic interactions may importantly structure ecosystems, prevailing ecological theory lies closer to the Gleasonian perspective. Holling (1992), however, proposed an extension of hierarchy theory that offers some simplicity and generality to ecology. Holling (1992) stated that the apparent complexity of ecosystem structure and dynamics is actually dominated, over

specific scale ranges, by the influence of only a small number of tightly coupled plant, animal, and abiotic processes. These processes operate at distinct frequencies and leave spatial imprints that entrain other processes (Holling 1992). In the following chapters, I attempted to evaluate the applicability of specific interpretations of the new, general theory that Holling (1992) proposed to wildfire and mammals of the boreal forest.

Three Theoretical Views of Ecosystems

For the sake of clarity it is useful to consider three theoretical perspectives of ecosystems: (1) a null model, (2) prevailing ecological theory, and (3) Holling's (1992) variation on hierarchy theory. The particular null model I will outline is an extension of Gleasonian theory. In this null ecosystem model, there is a one-way bottom-up flow of control stemming from abiotic conditions up through the trophic pyramid. Biotic interactions exist (e.g., herbivory, predation, parasitism, and competition), but are constrained by limits imposed by lower trophic levels. Predators, for example, do not structure their environment by importantly influencing the availability of their food source. Thus, an ecosystem is an arbitrary collection of species. Any spatial and temporal pattern in the distribution of species is also ultimately dictated by abiotic conditions. Further, there are any number of these factors that might be critical to controlling ecosystem structure. Of course, a single factor might emerge as limiting but, which is arbitrary, and almost any one is a potential candidate.

In great part, prevailing ecological theory (Begon et al. 1986, Real and Brown 1991) differs from this null model by recognizing that some biotic interactions cause important feedbacks that structure lower levels in the trophic pyramid. That is, some species importantly influence the conditions

of their own environment. Depending upon the system in question and school of thought, some systems are seen quite conservatively (close to the null model), while others are seen to possess so many, often independent, feedbacks that holistic understanding can be difficult or impossible (Allen and Starr 1982). So, it is presently understood that many more factors can be important to governing system dynamics and structure than the null model predicts (Begon et al. 1986, Real and Brown 1991). Because ecological systems are complicated in these ways, the development of general theory has been limited (Allen and Starr 1982).

The body of theory that Holling (1992) proposes differs significantly from prevailing ecological theory. First, it assumes ecosystems are structured hierarchically in the sense that Allen and Starr (1982) and O'Neill et al. (1986) advocate. However, Holling (1992) extends this theory by stipulating that over a given scale range, only a few factors govern an ecosystem. Each process operates at a periodicity separated from the others by at least an order of magnitude (Holling 1992). Holling (1992) also states that each of these processes leaves spatial imprints at distinctly differing scales. Slowly cycling processes create large structure and rapidly cycling processes create small structure (Holling 1992). Because structure is not being created at all scales in between, the net effect is that system structure will fall into specific size groups (Holling 1992). In a forest, for example, rapidly cycling physiological processes create small-scale structure in the leaves of herbs and grasses, and more slowly cycling plant competitive processes create structure at the scale of a tree gap (Holling 1992). Also important to the theory, is the assumption that at some range of scale, the biota (acting as one of the few controlling factors) modifies the environment in such a way as to bring about catastrophic renewal (Holling 1987, 1992). For example, the buildup of canopy volume in

the boreal forest of Eastern Canada sets the stage for spruce budworm (*Choristoneura fumiferana*) outbreaks (Holling 1980, 1986, 1987, 1992). As a result, forest age structure, patch size, and temporal dynamics all distinctly differ from that predicted by either the null model or any complex model of ecosystem structure.

Three Theoretical Views of Wildfire in the Mid-Continental Boreal Forest

Wildfire is, by far, the dominant disturbance process in the mid-continental boreal forest of North America (Heinselman 1973, Stocks and Street 1983, Suffling et al. 1988, Ehnes and Shay 1995, Suffling 1995). As such, fire must feature prominently in any theoretical explanation of system structure.

Fire ecology is currently attempting to understand the extent to which vegetation structure complicates the spatial and temporal pattern of fire occurrence. Attempts are being made to assess whether wildfire dominated ecosystems are like the null model, or more complex models involving strong biotic feedback. Some authors have emphasized the dominant role that climate and topography play in controlling the fire regime in northern coniferous forests (Johnson 1979, Bessie and Johnson 1995) and in the boreal forest specifically (Bergeron 1991, Johnson 1992, Dansereau and Bergeron 1993). Others have emphasized the role of fuel accumulation and increased burn hazard as stands age in controlling the fire regime in northern coniferous forests (Agee and Huff 1987, Clark 1988, 1989, 1990a, 1990b, Romme and Despain 1989, Holling 1980, 1986, 1987, 1992) and in the boreal forest specifically (Heinselman 1973, Rowe and Scotter 1973).

Whether through biotic or abiotic means, fire has been generally assumed to be controlled by many factors. If each of many factors has a small

effect on a system, then it would be predicted that metrics of system structure would fall into continuous distributions. Fires, for example, would tend to grow to some arbitrary size depending upon multiple, subtle effects of topography, relative humidity, wind, fuel dryness, chemical composition, density, and three-dimensional spatial distribution, etc. Fires would not be constrained to particular size categories other than the tendency for large fires to be rare. The net effect would be a continuous distribution of fire sizes.

Holling (1992), however, proposes a much simpler perspective. In application to the mid-continental boreal forest, the general theory proposed by Holling (1992) could be interpreted in two ways. It is possible that fire acts as one of a number of plant, animal, and abiotic structuring processes. The distinct periodicities over which these processes operate create characteristic sizes of forest patches. Taken together, they create a multimodal distribution of patch sizes in the forest. Alternatively, it is possible that fire itself is controlled by a small number of factors that operate at distinct periodicities. As a result, the distribution of fire sizes would be multimodal. Because fire has a dominant effect on forest structure, by itself, it creates a multimodal distribution of patch sizes in the forest.

It also seems that Holling's (1980, 1986, 1987, 1992) general proposal that the biota modifies the conditions within the system to bring about catastrophic renewal could be interpreted to be applicable to this region. Specifically, fuel accumulates as a stand ages and causes the burn hazard to increase. The time required for sufficient fuel to accumulate would thus regulate the return of fire to a given stand. The cyclic interaction of vegetation and fire would, in this way, define one of the key factors in the hierarchy of system control.

Alternative Theoretical Views of the Mammal Component of Boreal Forest Communities

A number of authors have examined general trends in the distributions of body sizes in animal communities for evidence of the fundamental rules by which ecosystems are structured (Hutchinson and MacArthur 1959, Van Valen 1973, May 1978, 1988, Dial and Marzluff 1988, Morse et al. 1988, Lawton 1990, Brown and Nicoletto 1991, Maurer et al. 1992, Blackburn and Gaston 1994, Brown 1995). For many diverse animal communities the unimodal, right-skewed character of these distributions has been noted and has been interpreted as evidence that many, stochastic factors structure ecosystems (Brown 1995). However, other authors (Griffiths 1986, Holling 1992, Holling et al. 1996, Manly 1996, Restrepo et al. 1997, Lambert and Holling in press) have indicated possible multimodality in body mass distributions and in other body-size metrics (Stubblefield et al. 1993). Holling (1992) attributed the multimodality in body sizes to an inferred multimodal size distribution of resource patches in the ecosystem. The relatively regular pattern of resource distribution causes the distribution of body masses of all species to cluster (Holling 1992, Hostetler 1997). Species within a cluster exploit resources at similar hierarchical levels (Holling 1992, Hostetler 1997).

Each of these very different theoretical perspectives has important implications for ecology. Improved understanding of ecological systems would be attained if the relative merit of each could be determined. While testing whether the entire circumpolar boreal forest is structured hierarchically in any fashion is beyond the scope of this study, I tested specific interpretations of the general body of theory proposed by Holling (1992) as they relate to wildfire and the mammal component of communities through several means.

Overview

Holling (1980, 1986, 1987, 1992) proposed that the biota plays a central role in controlling ecosystems by causing catastrophic renewal. If this general theoretical proposal applies to the mid-continental boreal forest at the landscape scale, then it should involve wildfire. Thus in chapter 2, I specifically tested whether burn hazard increases with stand age. The approach I took to testing this hypothesis was to gather spatially explicit fire data from a very large region of Southeast Manitoba over 63 years. With this large data set, I was able not only to directly measure burn hazard as a function of stand age, but to also characterize the general fire regime. I used these results to make some predictions regarding the potential effect of climate change on this region.

As previously discussed, current ecological theory predicts that metrics of system structure will fall into continuous or unimodal distributions. The body of theory that Holling (1992) proposes, however, predicts that metrics of system structure will be multimodal. Decisive testing whether the former or the latter is the case has been prevented by the lack of statistical tests appropriate for the detection of complex multimodality. When few, well-defined modes are expected, some existing methods can be used effectively, but not otherwise.

In chapter 3, I introduce LS as a new statistical method appropriate for the detection of complex multimodality. Any search for multimodality must distinguish aggregations defining real modes in the underlying distribution from data aggregations of random origin. LS avoids the problems inherent to past approaches that search for some "best" stopping rule attempting to separate real modes from random clusters. LS divides data aggregations over

many resolutions (i.e., degrees of smoothing) using kernel density estimates. Multimodality is indicated if the location of aggregations correlates amongst three or more data sets. The significance of such apparent matching is determined through simulation. Because LS effectively balances the detection of potential pattern (avoidance of type II error) with the need for statistical rigor (avoidance of type I error), it is generally the most appropriate method for detection of complex multimodality. After I demonstrated the mechanics, behavior, and power of LS, I used it to test for multimodality in the distribution of body masses in the mammal component of boreal communities in Eastern North America, Northern Europe, and Eastern Russia.

In chapter 4, I used LS to test whether the sizes of fires in the mid-continental boreal forest have a multimodal distribution. If so, this is argued as evidence that wildfire is controlled by a small number of factors that operate at distinct periodicities. Recall, however, that this is only one interpretation of how the very general body of theory proposed by Holling (1992) could be interpreted to apply to this system. In chapter 4, I also characterized some of the effect of climate on fire regime. The indications obtained regarding the role of climate and the degree of system complexity, provided another means to improve predictions of the effect of potential climate change on the mid-continental boreal forest.

CHAPTER 2
THE EFFECT OF LANDSCAPE-SCALE VEGETATION PATTERN ON BOREAL FOREST WILDFIRE IN SOUTHEAST MANITOBA, CANADA

Introduction

Fire ecologists are currently attempting to understand the extent to which vegetation structure complicates the spatial and temporal pattern of fire occurrence. Some authors have emphasized the dominant role that climate and topography play in controlling the fire regime in northern coniferous forests (Johnson 1979, Bessie and Johnson 1995) and in the boreal forest specifically (Bergeron 1991, Johnson 1992, Dansereau and Bergeron 1993). Others have emphasized the role of fuel accumulation as stands age in controlling the fire regime in northern coniferous forests (Agee and Huff 1987, Clark 1988, 1989, 1990a, 1990b, Romme and Despain 1989, Holling 1980, 1986, 1987, 1992) and in the boreal forest (Heinselman 1973, Rowe and Scotter 1973). Specifically, the latter group have argued that the burn hazard (i.e., the proportion of all forest stands that survive to, but burn at, a given age) increases as stands age. If burn hazard increases with stand age, then age structure, patch size, and temporal dynamics all differ from that expected when burn hazard remains constant (Johnson 1992, Peterson 1994, Ratz 1995). Thus, this single property has important implications for system structure and dynamics and its qualitative response to perturbation.

Wildfire, the Boreal Forest, and Climate Change

Wildfire is a key disturbance agent in the boreal forest and thus strongly influences its distribution, composition, and structure (Heinselman 1973, Johnson 1992, Pastor and Mladenoff 1992, Payette 1992, Sirois 1992, Stocks 1993, Kuhry 1994, Lavoie and Payette 1996). In the mid-continental boreal forest of North America, wildfire has an especially dominant effect (Heinselman 1973, Stocks and Street 1983, Suffling et al. 1988, Ehnes and Shay 1995, Suffling 1995). Wildfire in the boreal forest is usually catastrophic—it consumes litter, ground-level vegetation, and canopy vegetation in an intense, often large burn and thus exerts great influence over the biota (Johnson 1992). Seed sources are limited and accumulated litter is removed; thus wildfire governs soil and ecosystem development. Climate constrains fire regime over large scales. Local conditions determine whether point ignitions either self-extinguish or propagate from stand to stand to cover up to thousands of square kilometers.

Present assessment of global climate change projects a 1 to 3.5 °C increase in global surface air temperature by the year 2100 (Watson et al. 1995). Boer et al. (1992) largely concur, predicting a 3.5 °C increase in global surface air temperature and a 5-8 °C increase at high latitudes with a doubling of atmospheric CO_2. Effects upon precipitation are less certain but moderate increases have been projected for northern latitudes (Boer et al. 1992, Watson et al. 1995). The net effect, however, is that potentially substantial decreases in summer soil moisture are projected for northern continental regions (Manabe and Wetherald 1986, Singh and Wheaton 1991, Boer et al. 1992, Watson et al. 1995).

Under such a transformation, the boundaries of biomes are expected to shift; however, the speed and magnitude of these shifts are largely uncertain. Direct effects of climate change on the boreal forest may be significant, but it is strongly suspected that the primary agent of change will be wildfire. A number of authors predict dramatic increases in fire occurrence (Overpeck et al. 1990, Wein 1990, Flannigan and Van Wagner 1991, Stocks 1993, Wotton and Flannigan 1993, Hogg and Hurdle 1995). Improved understanding of the response of forests to potential climate change, however, would benefit by an improved understanding of fundamental ecosystem processes (Stocks 1993, Watson et al. 1995).

A Hierarchical View of the Mid-Continental Boreal Forest

According to hierarchy theory, ecosystems are composed of discrete scale ranges within which factors interact strongly and in relative isolation (Allen and Starr 1982, O'Neill et al. 1986). This perspective has been widely regarded as a useful heuristic because it permits the exclusion of many complicating factors from individual subsystems. Whether ecosystems actually are structured hierarchically, however, is still controversial. Despite this, Holling (1992) proposed an extension of hierarchy theory by arguing that over a given scale range, a unique set of only a few factors controls the system.

Holling (1980, 1986, 1987, 1992) also proposed that the biota (acting as one of the few controlling factors) modifies the environment in such a way as to bring about catastrophic renewal. If the latter general theoretical proposal applies to the mid-continental boreal forest at the landscape scale, then it should involve wildfire. The specific mechanism that may importantly influence this system then is this: fuel accumulates as a stand ages and causes the burn hazard to increase. The return of fire to a given stand would thus be

regulated by the time required for sufficient fuel to accumulate. In this way, the cyclic interaction of vegetation and fire would define one of the key factors in the hierarchy of system control. Presumably, other factors would dominate over smaller and much larger scale ranges in the overall hierarchy.

In this chapter, I propose an interpretation of the general body of theory that Holling (1980, 1986, 1987, 1992) advocated. Specifically, fire size is a function of the slow accumulation of fuel as each stand ages and fluctuating climatic conditions. Fires tend to be small until enough fuel has accumulated and climatic conditions favor the wide propagation of fire over the landscape. Thus, many small fires occur below this threshold and many large fires occur above it. A multimodal distribution of fire sizes should result. The periodic return of large fires would occur in cycles associated with fuel accumulation and climate. Although not located in a boreal site, an example from Northern Minnesota provided by Clark (1988, 1989, 1990a, 1990b) illustrates these points. Clark (1988, 1989, 1990a, 1990b) working with unique, very long term (750 yr) data sets, found distinct 11, 33-36, and 80-95 yr. periodicities in fire occurrence associated with climatic effects interacting with fuel buildup.

Knowing whether burn hazard increases with stand age will help understand how the mid-continental boreal forest is physically structured by fire. It also sorts between competing general theories of ecosystem control. In addition, it is hoped that it would provide some insight into how the boreal forest might respond to potential climate change.

An effective method for testing whether burn hazard increases with stand age measures stand age over a very large region at a reasonably high spatial resolution for decades or even centuries. I measured burn hazard directly in this study, and I also created maps and calculated indices characterizing the fire history of the study area. These maps and indices

include: a stand origin map, a map counting the number of times each stand burned, the proportion of the study area burned annually, the time-since-fire distribution, a frequency distribution of the number of times each stand burned, and the fire cycle. These indices assist the interpretation of the relationship between burn hazard and stand age and provide insight into the general fire regime.

Study Site

Because the center of the continent is likely to be most sensitive to potential climatic warming, the study site was situated in Southeast Manitoba, Canada (Fig. 2-1). It encompasses an approximately 26660 km^2 (163 km on a side) region located north of the town of Bisset between Lake Winnipeg and the Ontario border within the subhumid mid-boreal ecoclimatic region (Ecoregions Working Group 1989). The area is characterized by Canadian Shield substrates—coniferous forests dominate but deciduous species are common. Generally, the eastern portion of the study area is characterized by higher mean elevation, variable topography, a larger proportion of well-drained upland sites, and glacial deposits, whereas the western portion is characterized by flatter topography, a larger proportion of poorly drained lowland sites, and lacustrine deposits (Woo et al. 1977, Dutchak et al. 1978). The mineral soils of upland areas are dominated by jack pine (Pinus banksiana) but include white spruce (Picea glauca), trembling aspen (Populus tremuloides), paper birch (Betula papyrifera), and balsam fir (Abies balsamea; Woo et al. 1977, Dutchak et al. 1978). The often thick organic soils of lowland areas are dominated by sphagnum moss (Sphagnum spp.), black spruce (Picea mariana), and tamarack (Larix laricina; Woo et al. 1977, Dutchak, et al. 1978). Wildfire interrupts successional progression and

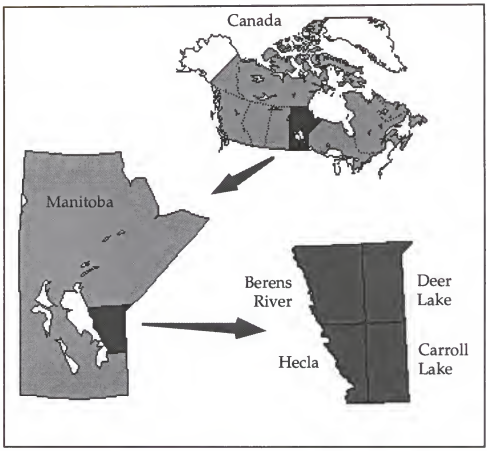

FIG. 2-1. The location of the study site within Southeast Manitoba, Canada. Each of the four subregions is also shown.

direct species replacement is typical (e.g., jack pine stands often regenerate from burned jack pine stands).

Fire is by far the dominant disturbance process within the study region. Manitoba Natural Resources (1986, 1991) indicates that of all stand-replacing disturbance, 92% is caused by fire, 4% is due to logging, and 4% is due to insect defoliation. Somewhat less than half of the study area (in the west and south) has been given a high degree of fire protection in recent decades while a low degree has been given to the rest (Glenn Peterson, personal communication). Though buildings and private property have certainly been saved, it is

unclear what the net effect fire protection has had on the forest (Glenn Peterson, personal communication).

The study area is very sparsely populated. A few, very small towns are concentrated in the south. Six small Indian Reservations are also within the study area, most of which are found along the shoreline of Lake Winnipeg. A sizable portion of the Southeast section of the study area encloses the Atikaki Wilderness Park within which fires have not been managed. Aside from logging roads, almost all transportation routes are restricted to the southern fringe of the study area. None traverse the study area, so much of the access to the eastern shore of Lake Winnipeg is accomplished by ferry across the lake from the more developed Interlake District.

Methods

Acquisition of data. To characterize the fire regime of the study area, I created maps summarizing the entire fire history. Fire maps explicitly recording annual fire perimeters between 1928 and 1990 were obtained from Manitoba Natural Resources (Manitoba Natural Resources: Forestry Branch, Forest Health and Ecology, Box 70, 200 Saulteaux Crescent, Winnipeg, Manitoba R3J-3W3). Manitoba Natural Resources recorded the outer perimeter of each fire as a tracing on 1:250,000 scale topographic map. The original 63 year record was thus divided amongst a series of maps for each of the study area's four topographic subregions: Hecla, Carroll Lake, Berens River, and Deer Lake (Fig. 2-1).

Creation of master fire map. To integrate these maps, I digitized them into a Geographic Information System (GIS). First each map was reduced to 44% of its original size. Using a light table, I made careful tracings of the fire perimeters on each map onto blank paper. Major coordinates were also

marked to enable later use of GIS rubber-sheeting and thus standardization of each map to a uniform map-projection, spatial extent, and resolution. These images were digitized using an AppleScan® scanner at 300 dpi. A paint program (UltraPaint™) was used to clean up the scanned images. The term "patch" is used in this study to refer to an area within a map (i.e., the full extent of a spatially connected portion of a map) that is distinct from other adjacent areas. The precise definition of a patch can thus differ depending on the particular attribute that a map specifies. The scanned images of fire perimeters typically contained patches that defined individual fires. However, fires sometimes overlapped and so patches would more correctly define a portion of the landscape with a unique fire history. Each of these patches was painted a different color. These images were then imported into the Map II® GIS where each patch was assigned a unique index number. These index numbers were also recorded in a Microsoft Excel® spreadsheet. The digital images were then converted into maps by GIS rubber-sheeting. Two majority-scans and a manual check were performed to reduce remaining distortions. The final digitized maps are accurate to approximately 0.0361 km^2 (190m on a side). A single forest stand in this study, then, is defined as 190 x 190 m area. To be explicit, patches can contain one or many individual, adjacent stands. For each topographic subregion in isolation, all the fire maps were integrated to get a complete 63-year fire history. Each patch on these summary maps records the years in which it was burned. Finally, each of the summary maps was joined into a single master map mosaic encompassing the entire study area.

Characterizing fire history. Simpler stand origin and burn count maps were derived from the master map using Map II®. Each patch of the stand origin map shows only the date of the most recent burn. Each patch of the

burn count map shows the number of times it has been burned. The information contained in the master map was also exported into Microsoft Excel® and manipulated to produce summary indices both to characterize the fire regime and to specifically test whether burn hazard increases with stand age. Summary indices include the proportion of the total area burned annually, the fire cycle, the time-since-fire distribution, the burn count distribution, and the burn hazard. The fire cycle simply measures the number of years required to burn an area equivalent in size to the study area just once. The time-since-fire distribution measured the proportion of the entire landscape escaping fire up to a given age. For comparison, I also created several randomized time-since-fire distributions. The magnitudes of the proportions were the same as those observed, but their order was changed; that is, the age to which each proportion of the landscape survives was reshuffled. The burn count distribution measured the number of times each portion of the landscape burned.

Calculation of burn hazard. The calculation of burn hazard was accomplished by calculating the proportion of all stands surviving to, but burning at, a given age. Because the age of unburned areas is unknown, these areas are omitted from the analysis. The rest of the landscape is composed of patches that have survived to 1990 or have reburned. The age of each of these patches can be calculated as either the age it reached in 1990, or the age it reached between burns. Summing over these patches calculated the total area at a given age when it burned or when data collection terminated in 1990 ($A'(t)$) as

$$A'(t) = \sum_{i=1}^{I_t} a_{ti} \qquad (2\text{-}1)$$

where I_t is the number of patches that reached age t, and a_{ti} is the area of just one of those patches. A more practical value than $A'(t)$ is the total area that ever survived to a given age ($A(t)$). $A(t)$ is simply a cumulative distribution of $A'(t)$ summed from oldest stands to youngest as

$$A(t) = \sum_{j=T}^{t} A'(j) \tag{2-2}$$

where T = 63 years, the oldest stand age and j specifies a given age. I also calculated the total area that reburned at a given age ($B(t)$) as

$$B(t) = \sum_{k=1}^{K_t} a_{tk} \tag{2-3}$$

where K_t is the number of patches that burned at age t, and k specifies one of those patches. Note again that $B(t)$ does not include any patch that burned only once because the age at which those areas burned cannot be determined. The burn hazard ($\lambda(t)$) follows as

$$\lambda(t) = B(t)/A(t). \tag{2-4}$$

With burn hazard calculated, a linear model was fit to its distribution in JMP® to determine whether any increase occurred as stands aged. I used JMP® and consulted Zar (1984) to perform an analysis of variance to determine the significance of the linear model's fit.

Results

Fire History

The stand origin map showing the year in which each patch was last burned indicates that most of the area burned is accomplished by very large fires (Fig. 2-2). The largest fires occurred in 1929—together they consumed 28% of the study area (7440 km^2 or 86 km on a side). Also evident are several areas where small fires are concentrated.

It is difficult to determine chronological pattern in the proportion of the study area burned annually (Fig. 2-3a). This chart does show, however, that since 1949, the annual area burned has not reached previous extremes. In Fig. 2-3b, it can most clearly be seen that very little area burns in most years. As we move to the highest ranked years, the area burned increases rapidly to the point where over half the total area burned occurs within three years (1930, 1948, and 1929 respectively).

The great part of the time-since-fire distribution closely follows a negative exponential distribution (Fig. 2-4a). It may be argued that two lines could produce a better fit over the distribution—the first including ages 1 to 43 years and the second including ages 43 to 62 years. However, the improved fit given by two lines would be marginal. The one data point that does not fit any trend is the last. This data point indicates that a disproportionately large part of the landscape burned in 1929. The area burned in 1929 was so great that much of it escaped reburning by 1990. As a consequence, the negative exponential curve seems to provide a poor fit. Also shown in Fig. 2-4b-d are a few randomized time-since-fire distributions. All of these charts indicate

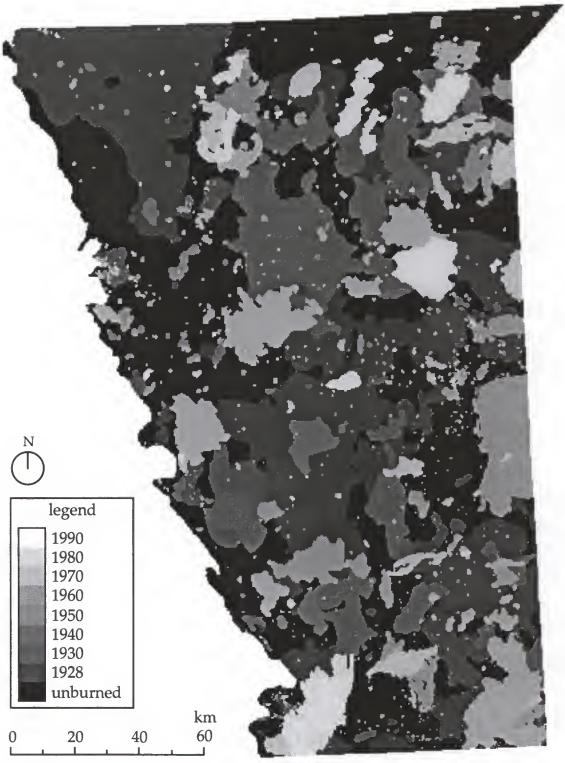

FIG. 2-2. The stand origin map indicating the dates of the most recent burn as of 1990 throughout the study area in Southeast Manitoba.

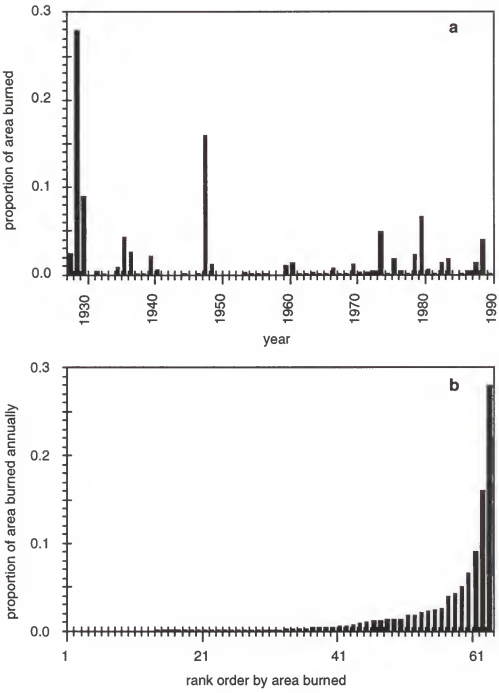

FIG. 2-3. The proportion of the study area burned annually: (a) in chronological order, (b) rank ordered.

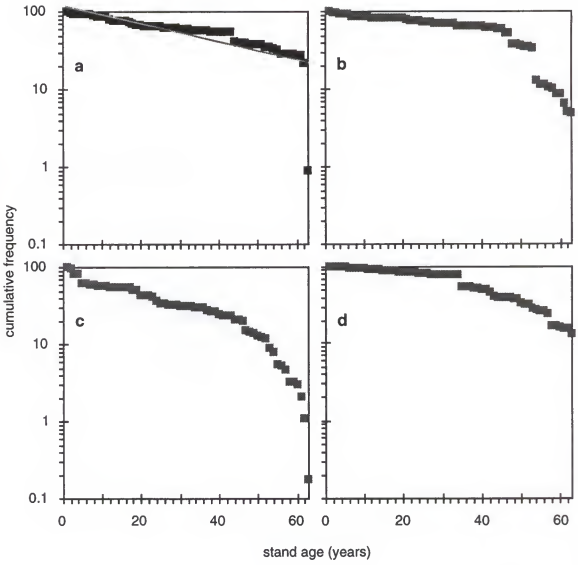

FIG. 2-4. (a) The time-since-fire distribution. This index measures the proportion of the entire landscape escaping fire up to a given age. A line has been fit to this distribution to indicate that most of the distribution seems to approximate a negative exponential. (b-d) Several randomized time-since-fire distributions are also shown. The magnitudes of the proportions were the same as those observed, but their order was changed; that is, the age to which each proportion of the landscape survives was reshuffled.

profoundly different fire regimes. Each indicates that at least two or three separate negative exponential distributions could be fit to them.

From the map of the number of times each patch of the landscape burned, one cannot easily discern a pattern in the spatial distribution of burns (Fig. 2-5). However, Fig. 2-5 indicates that there may be more reburns toward the eastern edge of the map. Because I determined how many times each portion of the landscape burned, I was able to calculate the number of years required to burn an area equivalent to the entire study area once (i.e., the fire cycle). Computing it this way, I found a fire cycle of 78 years within the entire study area. Therefore, the period over which data were gathered encompassed 81% of a fire cycle. Despite most of a fire cycle occurring, 36% of the region remains unburned, and 16% of the region has burned more than once (Fig. 2-6). The burn count distribution in each subregion varies from that of the entire region (Fig. 2-6). The fire cycle for each subregion was found to be 68, 74, 92, and 74 years for Hecla, Carroll Lake, Berens River, and Deer Lake, respectively.

Burn Hazard

Great variation over the entire burn hazard distribution is apparent (Fig. 2-7). Young stands seem to have a slightly lower probability of burning than older stands. A line fit to this distribution also indicated a slight increase in burn hazard with age (Fig. 2-7). However, $r^2 = 0.019$, so very little of the variation is explained by the fitted line. Furthermore, an analysis of variance found the fitted line insignificant ($P = 0.28$).

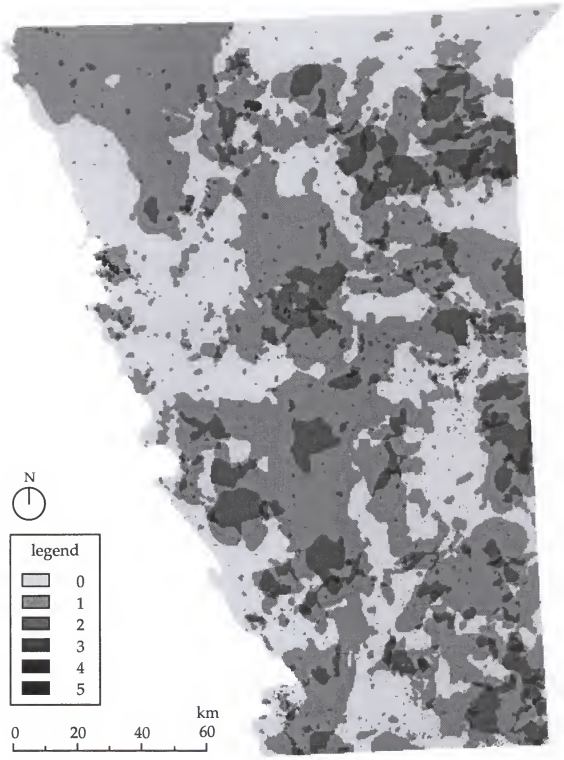

FIG. 2-5. The burn count map. The number of times each portion of the Southeast Manitoba study area burned between 1929 and 1990 is shown.

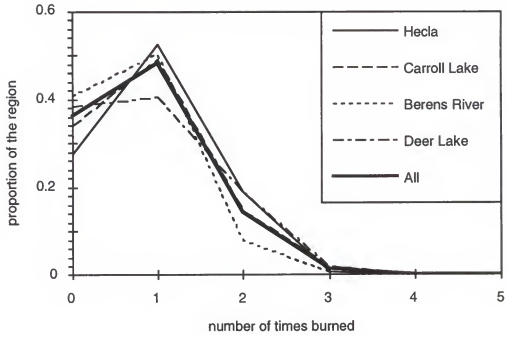

FIG. 2-6. The burn count distribution for the study area as a whole and each individual subregion.

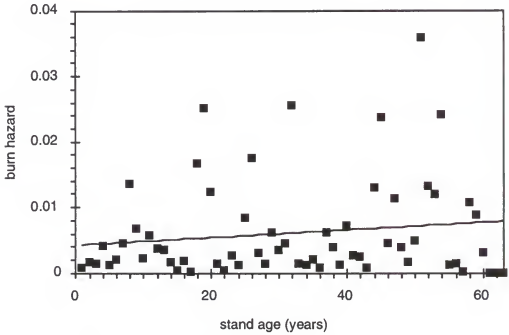

FIG. 2-7. The burn hazard distribution. Burn hazard measures the proportion of all forest stands that survive to, but burn at, a given age. The line fit to this distribution has the function: $\lambda(t) = 0.00427 + 0.00006(t)$ where $\lambda(t)$ is the burn hazard and t is the stand age.

Discussion

Fire History

Fire in the boreal forest acts over a very large area and long time span. Fire sizes tend to be very large (covering areas as large as 14000 km^2 or 118 km on a side), post-fire forests require decades or even centuries to achieve maturity, and fire cycles range between 50 and 200 years (Johnson 1992). As a consequence, large areas should be examined at a sufficient resolution over long time periods to reveal meaningful pattern in the landscape. It is fortunate that this has been well understood for such a long time by Canadian provincial governments. The long standing policy of Manitoba Natural Resources to record the spatially explicit perimeters of all fires in Southeast Manitoba has enabled me to create the maps shown in Figs. 2-2 and 2-5. From these maps, I was able to derive indices measuring the effects of fire on forest structure at the landscape scale.

It is less than ideal that the stand origin map shown in Fig. 2-2 differs from that given by Heinselman (1973) in that it was constructed from government fire records and not from direct photo-interpretation and field sampling. As a result, it contains patches for which the date of last burn is unknown and documents a limited 63-year time period. Another problem with these data is that virtually no unburned remnants were recorded inside the perimeter. The perimeter boundaries have also been somewhat simplified and distorted through the original documentation done by Manitoba Natural Resources and through the process of digitization. Thus, the articulation of individual fires is somewhat smoothed and their size has been slightly increased. Furthermore, the calculation of burn hazard makes

the assumption that all stand-replacing disturbance and regeneration in the study area occurs as a result of fire. It is likely that this assumption is reasonable, because mortality/regeneration events caused by other factors and covering spatial extents of one or more stands are comparatively minor.

The design of this study has important advantages over studies that use direct photo interpretation and field sampling. The very large area covered here permits a very high (i.e., annual) resolution in the time-since-fire distribution and a substantially reduced probability of sampling error for all indices. Also, the extent of repeat burns are recorded that enabled the direct calculation of burn hazard.

The complex mosaic of post-fire stands shown in Fig. 2-2 underscores the overwhelming importance of large fires. It is clear that while small fires are more numerous, taken together they account for a small percentage of the total area burned. Small fires can also be found to cluster in several areas along the shoreline of Lake Winnipeg and in the extreme southern end of the map. Two others can be seen in the middle of the map near the eastern edge. Most of these areas surround Indian Reservations and are probably evidence of arson-initiated fires intended to provide local employment in fire-fighting (Gerald Becker and Glenn Peterson, personal communication). The clusters of fires in the extreme south indicate the location of the town of Bisset and the path of highway 304. The majority of these fires are caused by human activities. Despite human effects, lightning-initiated fires account for 90% of the area burned within the boreal forest (Johnson 1992). The eastern shore of Lake Winnipeg is particularly subject to summer thunderstorms (Johnson 1992, Gerald Becker and Glenn Peterson, personal communication). Whatever their cause or point of origin, Fig. 2-2 seems to indicate that fires

spread to cover arbitrarily large areas and are widely scattered over the landscape.

It is understood that topography has an effect on site specific fire regime in the boreal forest (Johnson 1979, Stocks and Street 1983, Bergeron 1991, Dansereau and Bergeron 1993, Kuhry 1994). Better drained upland sites burn more frequently. As a result, distinct vegetation associations develop in upland and lowland areas (Bergeron 1991, Kuhry 1994). It is possible that some bias is introduced into this study because all topographic units are pooled. However, most of all stands that burned were burned by large fires and these tend to propagate over upland and lowland areas alike (Bergeron 1991, Dansereau and Bergeron 1993).

The proportion of the total area burned annually shown in Fig. 2-3a and b indicates the irregularity of wildfire activity. Little area is burned in most years and more than half the area burned is accomplished in just three years. It is possible that more effective fire protection in recent decades has prevented the extreme fire years found prior to 1949. However, the degree to which fire protection affects the fire regime is difficult to assess. For example, very large fires occurred in 1977 and 1989 on the western shore of Lake Winnipeg within an area of intensive fire management. The area burned annually in Canada between 1918 and the late 1980s was calculated by Van Wagner (1988) and Stocks (1991). They noted that despite great annual variability, a decreasing trend in area burned continued into the middle of the century; at which point, increases again occurred in spite of fire management efforts. Van Wagner (1988) and Stocks (1991) attributed this pattern to climatic effects. The results shown in Fig. 2-3a indicate that Southeast Manitoba may have followed these nation-wide trends.

General Indicators of Burn Hazard from Fire History

Some authors have argued that the shape of the time-since-fire distribution can detect whether stand age affects burn hazard (Van Wagner 1978, Yarie 1981, Johnson and Van Wagner 1985, Johnson and Larsen 1991, Johnson 1992, Finney 1995). If time-since-fire is plotted on a semi-log chart as in Fig. 2-4a, then a straight line would indicate that a negative exponential distribution of stand ages exists over the landscape. If the area burned annually is relatively constant and an arbitrary portion of the landscape is burned (i.e., stand age is unrelated to burn hazard), then over time a negative exponential distribution of stand ages would develop. The presumption is that if breaks (i.e., intervals with distinct slopes) cannot be assigned to climatic changes, then they may indicate increased burn hazard as stands age. That is, if climate does not vary (over periods greater than one year), the area burned annually is relatively constant, and the slope takes a distinct downturn after some decades, then this may indicate that stands tend not to burn until they reach a specific age.

The question is, however, is it ever possible to satisfy the assumptions that interpretation of the time-since-fire distribution requires? As I've already shown, the area burned annually is extremely variable. The results shown in Fig. 2-4 indicate that great care should be taken when interpreting time-since-fire distributions. Simple variability in area burned annually can produce distributions of stand ages that are very distinct from each other and from a negative exponential. As a result, it is unclear what the time-since-fire distribution can determine other than provide a snapshot of the present distribution of stand ages. Baker (1989) also discusses the limits that small

study areas, short time intervals, and temporal variation impose on interpretation of time-since-fire distributions.

If stand age exerts a great control over burn hazard then most of the study region should burn only once over the course of a single fire cycle. Fires initiated in young stands would tend to self extinguish, but fires initiated in older stands would tend to propagate themselves until they reach a barrier such as a lake edge or young stand. Eighty-one percent of a fire cycle occurred over the entire study area and yet much of it burned more than once or remained unburned (Figs. 2-5 and 2-6). Consider also that even though Carroll Lake and Deer Lake have the same fire cycle, they have quite different burn count distributions. If stand age tightly controlled burn hazard, I would expect that these distributions should be very similar to each other. Although, by themselves, these results are not conclusive, they are suggestive that stand age does not have a great effect on burn hazard.

Direct Measure of Burn Hazard and its Implications

Taken together, these informal tests seem to indicate that fires burn over old and young stands alike. In a more formal treatment, the calculated relationship between burn hazard and stand age was found to be insignificant. Therefore, the size a fire reaches is essentially unaffected by stand age. The likely explanation for this result is that postfire stands in the boreal forest are characterized by leftover unburned fuel, rapid accumulation of small-diameter herbaceous surface fuels, and dense re-establishment of seedlings from a large jack pine and black spruce serotinous cone seed bank. Stands may be slightly less likely to burn in the first few years following fire (Fig. 2-7). However, a small proportion of the total area of the boreal forest is very

young at any given time, so this phenomena has, at most, minor consequences.

At landscape scales in the mid-continental boreal forest, the area burned by any given fire or over a fire season thus seems to be largely determined by the degree to which climatic factors are conducive to the contagious spread of fire from one stand to the next. At smaller scales, a different set a factors (e.g., weather and/or topography) may dominate, but those are not examined here. It is at the landscape scale, however, that fire acts and in great part determines the species composition and stand structure of the boreal forest. While I have made no effort here to examine the effects of species composition, it seems that vegetation structure exerts no meaningful feedback control on fire size. Thus, in the mid-continental boreal forest and over the range of scales examined, the biota does not modify conditions in the system in a way that brings about catastrophic renewal as Holling (1980, 1986, 1987, 1992) hypothesizes. Further, the mechanism by which I hypothesized fires might be constrained to a multimodal size distribution has been disproved. This does not mean that the mid-continental boreal forest is not hierarchically structured in the manner that Holling (1992) suggests. It does, however, eliminate one specific mechanism that may have contributed to making it so.

All of these conclusions are valid within the context of the range of climatic conditions occurring through the greater part of the twentieth century. It is not possible, however, to predict with certainty how the system will behave under unique climatic conditions. Climatic change models predict higher temperatures with a high degree of confidence, but predict regional precipitation with lower confidence (Boer et al. 1992, Watson et al. 1995). If precipitation is substantially increased, then it is possible that the

overall burn hazard may be decreased and the slightly lower burn hazard of young stands could have a more important effect. If, however, climate change is characterized by an increased frequency of the kind of extreme fire years we already have seen, then its immediate effects will be little complicated by vegetation age structure. Longer-term predictions are less certain though. If cumulative effects of climate change dramatically alter the species composition of the forest or preclude forest altogether, the rules governing the fire regime will also be likely to change.

Conclusions

Because boreal forest wildfire acts over large spatial and temporal scales, studies benefit by encompassing very large areas and/or time spans. Although this study was limited to 63-years, it encompassed a very large area with spatially explicit fire data. The examination of pattern in both time and space has permitted a clear test of whether burn hazard is a function of stand age and examination of fire regime more generally.

With regard to the fire regime in general, I found that the great majority of the area burned was accounted for by large fires that occurred in just a few years. It seems that annual and possibly decadal climatic conditions greatly alter total area burned. It also seems that caution should be used when interpreting time-since-fire distributions. This is because simple variability in the annual area burned can misleadingly indicate distinct fire regimes spanning much longer time periods.

The burn count distribution seems to indicate that burn hazard is not strongly related to stand age. A more formal test measuring burn hazard directly indicates that although it increases slightly with stand age, this relationship is not significant. Therefore, stand age does not exert a feedback

control over fire. Contrary to Holling (1980, 1986, 1987, 1992), this implies that the biota does not modify conditions in the system in a way that brings about catastrophic renewal over the range of scales examined in the mid-continental boreal forest. This also disproves one specific mechanism that may have contributed to structuring the mid-continental boreal forest in a hierarchical fashion. Furthermore, existing vegetation age structure will not complicate the emergent fire regime in the short term insofar as potential climate change creates conditions similar to those of extreme fire years of the past.

CHAPTER 3
DETECTION OF COMPLEX MULTIMODALITY IN ECOLOGICAL DATA

Introduction

Advancements in ecological understanding are, in part, contingent upon discovery of patterns in community metrics. For example, general trends in the distributions of body sizes in animal communities have been examined for evidence of the fundamental rules by which ecosystems are structured (Hutchinson and MacArthur 1959, Van Valen 1973, May 1978, 1988, Dial and Marzluff 1988, Morse et al. 1988, Lawton 1990, Brown and Nicoletto 1991, Maurer et al. 1992, Blackburn and Gaston 1994, Brown 1995). The unimodal, right-skewed character of these distributions has been noted for many diverse animal communities and is interpreted as evidence that many stochastic factors structure ecosystems (Brown 1995). Other work, however, has indicated possible multimodality (or lumpiness) in body mass distributions (Griffiths 1986, Holling 1992, Holling et al. 1996, Manly 1996, Restrepo et al. 1997, Lambert and Holling in press) and in other body-size metrics (Stubblefield et al. 1993). Holling (1992) argues that multimodality in species body mass distributions is the structural signature of only a few processes dominating ecosystem dynamics.

Whether species body mass distributions are multimodal or not has remained an open question because the statistical methods used to detect complex multimodality are questionable. Notably, Holling (1992) detected as many as eight modes in distributions of birds and mammals of the Eastern

North American boreal forest and prairie using the Body Mass Difference Index. Manly (1996), however, clearly demonstrated some of the weaknesses of this test and found suggestive evidence for no more than two modes applying the more rigorous and conservative Silverman bump hunting technique to the same data sets. The methods employed by Griffiths (1986), Stubblefield et al. (1993), Holling et al. (1996), Restrepo et al. (1997), and Lambert and Holling (in press) indicate interesting support for multimodality, but they lack sufficient rigor to be statistically convincing. Each of these approaches has its strong and weak points. While Manly (1996) emphasizes the value of statistical rigor (avoidance of type I error), the other authors emphasize the detection of potential pattern (avoidance of type II error). Good scientific method advises a balance between the two. In the next section, I will discuss problems inherent to statistical tests for complex multimodality that surprisingly often have more to do with assumption than computation. I will then introduce a new statistical method appropriate for the detection of complex multimodality.

Statistics and the Detection of Complex Multimodality

Statistics attempt to separate signal from noise. Effective detection of complex multimodality requires that genuine modes be distinguished from random aggregations. Consider the density estimates of four data sets shown in Fig. 3-1. Depending on what resolution I choose to examine the data, I find 1, 2, or many potential modes. The question is, which resolution defines real modes beneath which remaining aggregations are of random origin?

A number of methods have been proposed to find multimodality: the Silverman bump hunting method (Silverman 1981, 1986), Penalized Likelihood method (Good and Gaskins 1980), Dip Statistic (Hartigan and

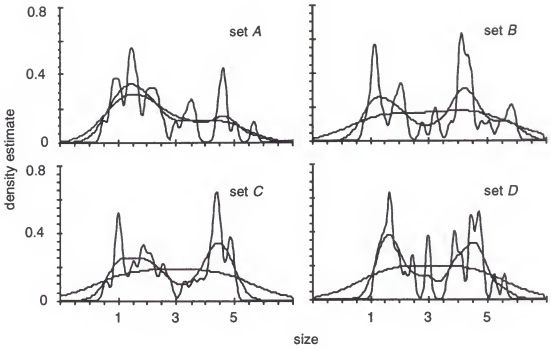

FIG. 3-1. 1, 2, and 10-mode normal kernel density estimates of data sets *A*, *B*, *C*, and *D*. Note that a density estimate measures the local concentration of data along the size axis. So if many data points occur within a short interval along the size axis, then the density estimate will be high. At each resolution, different aggregations are revealed. Each aggregation is either of random origin, or it indicates a mode in the distribution from which these data sets were sampled. Determining which resolution best defines each data set's modality is often a challenging problem. Also note that the size axis extends below 0 throughout this chapter because the data sets were derived from log body mass.

Hartigan 1985), Excess Mass Estimate (Muller and Sawitzki 1991, Polonik 1995), RUNT test (Hartigan and Mohanty 1992), MAP test (Rozal and Hartigan 1994), and a modified Silverman bump hunting method (Fisher et al. 1995). Each of these methods may be used with varying effectiveness, but their ability to detect complex multimodality is unknown because any power tests provided in the literature restrict themselves to simple distributions.

Although clusters are not synonymous with modes, cluster analysis may offer an alternative method for identification of lumps. Milligan and Cooper (1985) reviewed the ability of clustering methods for determining the number of clusters in a data set. They identified a few stopping rules that tend to reliably identify the correct number of clusters. However, these tests were again restricted to well-defined clusters (well-defined here meaning well separated clusters or modes with a high degree of internal cohesion). Bock (1985) reviewed some of the difficulties associated with detecting real clusters in heterogeneous distributions. It is not only a problem of how many clusters are in a data set, but also of idiosyncratic results obtained through the application of alternative linkage rules.

Generally speaking, there are three types of problems encountered when testing for multimodality: (1) sampling error, (2) conservative or intuitive interpretations of Ockham's razor, and (3) statistical methods designed to find only well defined modes. Sampling error is the tendency to under- or over-represent any feature of a distribution. The result is that real structure is obscured by a whole new level of spurious structure. The modal structure of a distribution can then only be viewed through the faulty lens of a sample. The obvious solution is to increase sample size wherever possible. If data sets have relatively few modes, this may not be a problem. If any number of modes is possible though, it may be argued that data are always limiting. While ultimately, this problem may never be solved, it may be possible to test a data set for any number of modes up to some arbitrary limit. This is the approach advocated here.

Difficulties can also arise when an excessively conservative interpretation of Ockham's razor is utilized. Ockham's razor is the accepted and generally effective procedure by which simple explanations are given

great preference over complex alternatives. The number of modes a distribution has is one measure of its complexity. If a given statistical method can show that a distribution seems unimodal, this explanation tends to be greatly preferred to any other. This paradigm pervades interpretation of results and even the design of the statistical methods themselves. The Silverman bump hunting method, for example, is designed to sequentially test for an increasing number of modes (beginning with unity). The problem is that idiosyncrasies in the distribution of data can cause the testing procedure to derail and underestimate the true number of modes. Thus, "for a multimodal distribution the probability of estimating the correct number of modes may be quite small" (Manly 1996). It's not that Ockham's razor does not apply to any search for multimodality. It is often appropriate to favor unimodality over multimodality or few modes over many. When sample size is limiting, for example, it is generally advisable to err on the side of conservatism. However, even high degrees of multimodality should be tested for and given due consideration. The latter is particularly true for metrics of complex or chaotic systems.

The third problem, that statistics have been developed to find only well defined modes, occurs for both practical and aesthetic reasons. The statistical detection of modes actually relies on the detection of sample clusters. Clusters are aggregations of data whereas modes are features of the underlying theoretical distribution. That is, modes are local maxima in the distribution from which the data set was sampled. Typically, major features (well defined modes) should be well represented as important clusters in sample data sets of adequate size. Important clusters are identified as those that stand apart from others according to a data-density measure (i.e., a metric indicating the local concentration of data). Minor clusters must then, by

procedural necessity, be dismissed from consideration. Moreover, a distribution containing modes of varying degrees of definition is intuitively more complicated than one with an equal number, but well defined modes. Again, according to Ockham's razor, the former is less attractive than the latter. In fact, real distributions can contain multiple modes with varying degrees of definition. Poor definition then, should not automatically remove modes from consideration. Past approaches to detection of multimodality have concentrated on the question, "Is a major cluster a mode?" In response, I have to raise the question, "Why is a minor cluster not a mode?"

In this paper, I will introduce a new statistical method, Lump Simulation (LS), that minimizes these problems and is therefore appropriate for the detection of complex multimodality. After I describe the mechanics and behavior of LS, I will apply it to the mammal body masses of the Eastern North American, Northern European, and Eastern Russian boreal forests.

Lump Simulation

A Brief Overview

An LS experiment determines the number of modes possessed by a group of three or more data sets. A series of pairwise tests between data sets is performed that compares the location of data clusters. Because clusters change as a function of the resolution at which the data are examined, a range of resolutions is examined. Thus, for each pair of data sets and each resolution, the degree of mismatch in the location of data clusters is calculated. The significance of each of these mismatches is determined (in a comparison-wise manner) by comparing the observed values to those expected from simulated data. To control for the experiment-wise error rate, I

searched for consistent matching over multiple pairwise tests at a specific resolution.

Experimental Design: an Example

To illustrate the mechanics of the method, I created four (n = 34) data sets, *A*, *B*, *C*, and *D* (Fig. 3-1 and Appendix), each of which is a random sample from a single bimodal distribution. This bimodal distribution (shown in Fig. 3-2a) has been fit to the Eastern North American, boreal-forest, mammal, log body-mass distribution (Holling 1992). To be specific, this distribution is the best-fit, bimodal, normal, kernel-density-estimate (Silverman 1981, 1986). Note that the sample size of boreal-forest mammal data set (n_{NAbm}) is 34 (see Appendix A). Also note that data sets *A*, *B*, *C*, and *D* were screened from a pool of simulated data sets such that they gave fairly good correlation by eye when viewed at a resolution giving 2 lumps.

Just to be clear, for the purposes of this exercise, I am not presently concerned with how many modes there really are in the observed mammal data set. That problem will be dealt with later. For the moment I simply need to demonstrate how LS works. As such, I will force this data set to have 2 modes and then test whether LS can discover this bimodality naively.

In general, LS achieves positive results only if the data sets used are samples from the same underlying multimodal distribution (or from similar multimodal distributions). Negative results imply that some of the data sets either come from distributions possessing unimodal structure or distinctly different multimodal structure. I must be careful then to include only data sets that are shaped by the same or very similar conditions. Sets *A*, *B*, *C*, and *D* form what is termed here an experimental group. In this case I know these sets come from the same underlying distribution. Often, under more realistic

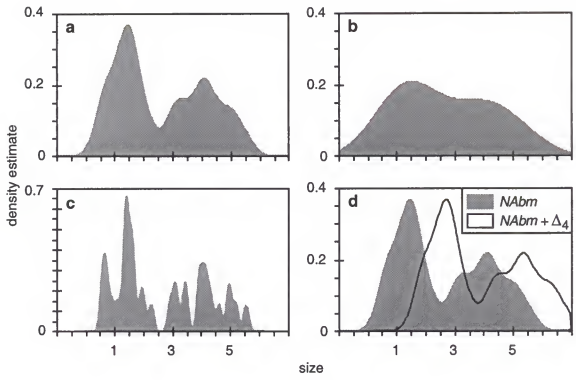

FIG. 3-2. Sampling distributions used in the example exercises. (a) the bimodal distribution fit to Eastern North American, boreal-forest, mammal, log body-masses (*NAbm*), used to create sets *A*, *B*, *C*, and *D*, and used in power tests to create all A^2, B^2, C^2, and D^2 sets, (b) the unimodal null sampling distribution fit to *NAbm* and used to create all A^1, B^1, C^1, and D^1 sets, (c) the 10-mode distribution fit to *NAbm* and used in power tests to create all A^{10}, B^{10}, C^{10}, and D^{10} sets, and (d) two bimodal distributions fit to *NAbm*—one is unaltered and the other (*NAbm*+Δ_4) is offset by 0.5*d* (where *d* is the distance between the modes) which puts these two distributions completely out-of-phase.

circumstances, this will not be the case and the researcher must infer, based on his understanding of the system in question, that these sets belong to a single group before proceeding.

Although sets *A*, *B*, *C*, and *D* genuinely have 2 modes, under normal circumstances I don't know this and therefore don't know what resolution to examine the data (i.e., which modal structures to test). For that reason, I will try many possibilities. The resolution that produces a consistent modal

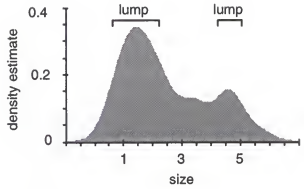

FIG. 3-3. The best-fit, 2-mode, normal kernel density-estimate of set *A* with lump intervals identified. Lumps, then, are segments along the size axis straddling local maxima of data-density. Any segment not identified as a lump qualifies as a gap interval, including the intervals extending to positive and negative infinity.

structure amongst data sets may indicate the true number of modes. If LS is effective, the 2 mode case will emerge as the best candidate in each data set in my example.

Calculation of Observed Mismatch

The procedure begins with the calculation of frequency distributions of the observed data using normal kernel estimates. A kernel estimate is simply a smooth histogram (Silverman 1986). Much like varying the bin width of a histogram, a parameter controlling the degree of smoothing (Silverman 1986) can be varied to reveal fine details of the distribution of density or gross features. When the smoothing parameter is large enough, any data set appears unimodal; but as it is decreased, more and more modes appear until eventually a normal-shaped mode appears for each nonidentical data point. Any data set then can have 1 through *n* modes (where n is the sample size and no data points are identical) forced upon it depending upon the resolution with which the researcher wishes to examine the data. For any

FIG. 3-4. Of three nominal data sequences, which pairing is more closely correlated? The phi coefficient (Wherry 1984) gives a an index of correlation for *X* vs. *Y* and *X* vs. *Z* of 0.45. My eyes, however, tell me that *X* vs. *Z* should be more correlated.

specified number of modes, the best-fit kernel estimate is one in which the degree of smoothing is just great enough to give that number of modes and no more (Silverman 1986).

The density information contained within the frequency distributions is then collapsed into two nominal categories (lumps and gaps). Each discrete location along the size axis, is classified as lump, if dense, and gap, if sparse (Fig. 3-3). To be more precise, I defined lumps as the interval surrounding and including a single local maximum (or mode). The exact limits of that region will be defined by the inflection points giving maximal and minimal slope. All other intervals along the size axis are then classified as gaps, including the intervals extending to positive and negative infinity at each end of the distribution.

Once the data sets have been classified into lumps and gaps, their lump structure (i.e., number and location of lumps and gaps) is correlated and its consistency evaluated. A correlation measure appropriate for nominal scale (i.e., lump or gap) is required. The phi coefficient index of correlation (Wherry 1984) could be used effectively to perform pairwise correlations between nominal data sets, but I found it lacking in its ability to distinguish

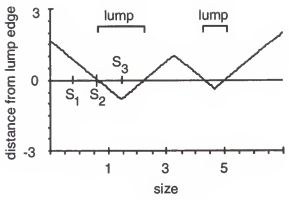

FIG. 3-5. The distance-from-nearest-lump-edge measure for set A with 2 lumps. This means, quite simply that S_1 is 0.8 units away from the nearest lump edge at S_2. Distance-from-nearest-lump-edge is negative inside a lump simply for graphic illustration. S_3 then, is again 0.8 units from the nearest lump edge.

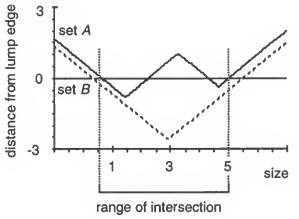

FIG. 3-6. The distance-from-lump-edge measures for set A with 2 lumps and set B with 1 lump. Also shown, is the range-of intersection between these two data sets (the range within which both data sets contain data). The range-of-intersection provides arbitrary boundaries within which the lump structure of these two data sets is compared.

near from complete misses. In the sequence shown in Fig. 3-4, which data sets are more correlated? My eyes tell me that sequence *X* is more closely correlated to *Z* than *Y*, but the phi coefficient finds no difference. So I created a distance measure that evaluates the differences between these cases in a manner more representative of what my eyes tell me. An example of how this distance measure is calculated for sets *A* and *B* is described below (Figs. 3-5 to 3-7).

The first step is to calculate the distance-from-nearest-lump-edge for each location along the size axis (Fig. 3-5). This distance-from-nearest-lump-edge measure is what provides the ability to distinguish between near and complete misses. In a similar manner to which the phi coefficient quantifies the correspondence or non-correspondence of nominal intervals, I will quantify lump and gap intervals. The difference is that instead of simply summing the number of intervals that correspond (or not), I will sum the distances. That is, rather than weighting each discrete location along the size axis equally, I weight its contribution to the total correspondence (or non-correspondence) by its distance-from-nearest-lump-edge.

Now if the distance-from-nearest-lump-edges for sets *A* and *B* are transposed upon one another (Fig. 3-6), I can begin the process of calculating the index of correlation. For the moment, I will concentrate on the case where there are 2 modes in set *A* and 1 mode in set *B*. Fig. 3-6 calls attention to the interval of comparison; that is, the interval over the size axis defined by the intersection of the range of set *A* and the range of set *B*. I will confine the analysis to the intersection of range.

If I sum up the area below 0 over the range of intersection for both curves, I get what is defined as the total lump area (a_L: Fig. 3-7). Similarly, if I sum up the area above 0 over the range of intersection for both curves, I get

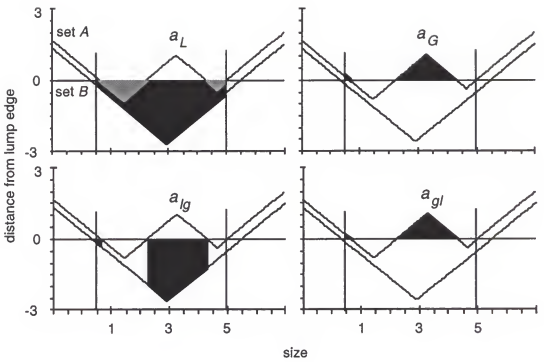

FIG. 3-7. The four subcomponents needed to calculate mismatch (m). Total lump area (a_L) is the sum of the area below 0 over the range of intersection for both curves. Similarly, total gap area (a_G) is the sum of the area above 0 over the range of intersection for both curves. Total area of lumps-in-gaps (a_{lg}) is the sum of the area below 0 for both curves in which lump intervals intersect gap intervals. Total area of gaps-in-lumps (a_{gl}) is the sum of the area above 0 for both curves in which gap intervals intersect lump intervals.

what is defined as the total gap area (a_G: Fig. 3-7). To quantify the mismatch between these two data sets, I first sum up all the area below 0 for both curves in which lump intervals intersect gap intervals (this defines a_{lg}: Fig. 3-7). Next, I sum up all the area above 0 for both curves in which gap intervals intersect lump intervals (this defines a_{gl}: Fig. 3-7). The proportion of gaps filled by lumps (p_{gl}) is then

$$p_{gl} = a_{gl}/a_G \tag{3-1}$$

where a_G = 1.11 and a_{gl} = 1.11, p_{gl} = 1.00 in my example. The proportion of lumps filled by gaps (p_{lg}) is

$$p_{lg} = a_{lg}/a_L \tag{3-2}$$

where a_L = 7.52 and a_{lg} = 4.36, p_{lg} = 0.58 in my example. The calculation of total mismatch (m) then is

$$m = (p_{gl} + p_{lg})/2 \tag{3-3}$$

which, in this example, gives m = 0.79. Thus m varies between 0 and 1 where 0 is a perfect match and 1 indicates complete mismatch. In this example, where I forced 2 modes on A and 1 on B, has thus proved to give a high degree of mismatch.

Recall that because I don't know how many modes really are in a data set, I cannot know a priori how many modes should be permitted in the kernel estimate. In other words, I don't know what resolution best separates signal from noise. Thus, a more complete picture of how well the lump structures of sets A and B correlate is obtained by testing at a number of resolutions up to some arbitrary limit (k modes). Recall that each set in this experimental group should have the same or very similar lump structure (at the correct resolution). If they have exactly the same structure, and if sampling error is not a concern, I could test only the cases where the number of lumps is equal in each set. In that case, I could test the 2 vs. 2, 3 vs. 3, ...k vs. k mode cases exclusively (later, I will explain why 1-mode cases are omitted). Typically, however, I should allow for some imperfection in the match. An arbitrary inequality of 1 lump is permitted here although higher values could

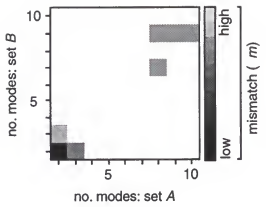

FIG. 3-8. The observed mismatch (m_{ij}) of sets A and B over all resolutions giving up to 10 modes.

be considered. Thus the 2 vs. 2, 2 vs. 3, 3 vs. 2, 3 vs. 3, 3 vs. 4, 4 vs. 3, ...k vs. k mode cases are all examined forming $3k$ - 5 comparisons (which is 25 in this example). For each comparison, I calculate m_{ij}, where i here gives the number of modes in set A and j gives the number of modes in set B (Fig. 3-8). In this experiment I will examine up to 10 modes.

It would be convenient if I could evaluate the degree of match at each resolution simply by calculating m_{ij}; however, I don't know how a given m_{ij} compares to that obtained by data sets randomly sampled from unimodal distributions. This measure of significance would give a true indication of whether or not data sets match exceptionally well. This is the step I will examine in the next section.

Determination of the Significance of Mismatch

To test the significance of each comparison's observed mismatch, I compute a distribution of expected mismatches. The supposition is that if I observe much less mismatch than expected, I have a significant match.

The calculation of expected mismatches depends intimately upon the null model of the distribution of sizes. Many possibilities exist, but for this example, I will use the unimodal, normal, kernel-density-estimate of the Eastern North American, boreal-forest, mammal, log body-mass distribution (Fig. 3-2b) as the null sampling distribution for each data set. The important requirement is that each null distribution be a reasonable unimodal representation of each data set. It should also be noted that the null distribution need not be the same for each data set. In fact, as I shall show later, it is often preferable in more realistic situations to improvise and calculate a unique unimodal distribution from each data set's own data. Simulated data sets (A^1 and B^1) with the same number of data points as the observed data sets are then randomly sampled from the null distributions (note that superscripts are used in the context of this chapter both to distinguish simulated data and to report the number of modes in the sampling distribution). For A^1 and B^1, I calculate the mismatch of each comparison (m_{ij}^1). A distribution of these expected mismatches (unique to each comparison) is found by repeating this procedure for 1000 pairs of simulated data sets. For a given comparison's distribution of expected mismatches, I can find a critical mismatch below which 1 or 5% of the curve's area is found. Thus the tail at the low end of the mismatch distribution including 5% of area of curve directly corresponds to a comparison-wise alpha level (α_c) of 0.05. For each comparison in turn, I can determine the significance of each observed mismatch by comparing it to the critical expected mismatch for the chosen comparison-wise alpha level. In this exercise, I will proceed using the commonly accepted significance level of 0.05. Fig. 3-9 (test 1) shows the results of evaluating the significance of each comparison of sets A and B. Note that the 2 vs. 2 mode comparison is the

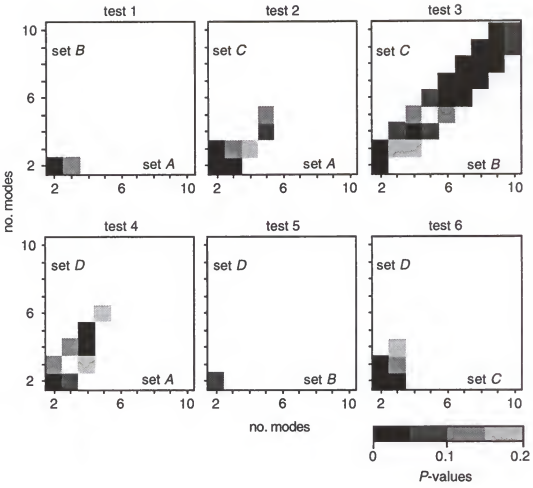

FIG. 3-9. The match significance for all comparisons in all tests in the LS experiment examining sets *A*, *B*, *C*, and *D*. Note that significance here is evaluated in a comparison-wise manner.

only comparison found significant.

Determination of significant matching in this manner doesn't work for 1-mode cases, however, because the sampling distribution is created from the 1-mode representation of the observed data. As such, the degree of mismatch found in the observed data would lay in the middle of the distribution of expected mismatches and thus would fail to reach significance. This is the reason LS examines a range of resolutions but omits the 1-mode case. This is

TABLE 3-1. Search results obtained (when $S_{c\,cv} = 0.75$) in the experiment examining sets *A*, *B*, *C*, and *D*. In test 1, the 2-mode case is found significant in both data sets (Fig. 3-9), thus significance count is 2 and $S_{c2} = 1.00$. No other modes are found significant, however, so the search limits have been reduced to the 2-mode case only. For this reason, only the 2-mode case is displayed here while 2-10 modes are tested. The 2-mode case continues to be found except in test 5 at which point the search consistency decreases but not below the critical value.

			no. modes
	test no.	test	2
significance	1	A / B	2
count	2	A / C	2
	3	B / C	2
	4	A / D	2
	5	B / D	0
	6	C / D	2
search	1	A / B	1.00
consistency	2	A / C	1.00
(Sc)	3	B / C	1.00
	4	A / D	1.00
	5	B / D	0.80
	6	C / D	0.83
search limits	1	A / B	x
	2	A / C	x
	3	B / C	x
	4	A / D	x
	5	B / D	x
	6	C / D	x
conclusion	-	-	0.83

not a serious problem though, because I will conclude that unimodality exists wherever multimodality is not found.

Now consider the degree of matching found for all comparisons in all tests. The order in which these tests are performed is arbitrary and must be decided before the analysis begins. It is visually apparent in Fig. 3-9 that the only relatively consistent pattern through all the tests occurs where each data

set has 2 modes. The last step in the experiment will quantify this apparent consistency by evaluating its significance formally.

Searching for Consistent Pattern

To come to firm conclusions about whether or not apparent consistency in the modal structure is significant, I have to control for the experiment-wise error rate. That is, I must evaluate whether or not the degree of match consistency is exceptional compared to that found with randomly simulated experiments. Note that the number of pairwise tests (Γ) is found by

$$\Gamma = \sum_{\gamma=2}^{M} (\gamma - 1) \tag{3-4}$$

where M is the number of data sets and γ is a simple counter. With $M = 4$, I have $\Gamma = 6$ in this example. By running $3k$ - 5 comparisons in a test and Γ tests, I am bound to get some significant comparisons at random. This is because significance has, so far, been evaluated in a comparison-wise manner. That is, each comparison has a 5% chance of being significant; thus I have an average of $\alpha_c\Gamma(3k - 5) = 0.05 \cdot 6 \cdot 25 = 7.5$ comparisons that will be significant at random in this experimental procedure. To control for this problem, I will integrate the results from each pairwise test sequentially in the remainder of this LS experiment. I will calculate the overall experiment-wise type I error rate (i.e., the P value) as the chance of consistently finding any modes significant (through all the comparisons and tests) in experiments using randomly simulated data sets. The maximum acceptable experiment-wise type I error rate (α_e) will be set at 0.05. Recall that this is the same value that I

chose for α_c. Although these values are the accepted standard, they should not be considered immutable and they need not even be equal. Lipsey (1990) gives an excellent discussion on the need to consider the trade-offs between statistical power and alpha level. Under certain conditions, it may be preferable to set a minimum power level and allow alpha to vary—even up to levels markedly higher than 0.05 (Lipsey 1990).

If I restricted the entire experiment to 2 data sets and a single comparison, the experiment-wise error rate would equal the comparison-wise error rate. The chances of testing the correct number of modes in each data set would, however, be very small. To increase the chances of including the correct comparison, I must expand the search limits. In any given test, the more comparisons I permit in the analysis, the greater the chance that I will get significance at random. Thus the experiment-wise error rate increases with the range limits of the search. To minimize experiment-wise error rate while achieving reasonable search limits, I will use the results of early, wide search limits in the first tests, to restrict the search limits in later tests. Results of early tests will be used to predict later ones.

As I begin searching test 1, I will set the search limits naively and accept any significant comparison (i.e., the search limits for each data set include 2-10 modes). To work through the example, I must examine Fig. 3-9 and Table 3-1 simultaneously. In test 1, I find the 2-mode case significant twice (once in each data set). No other modes give significance, however, so I will cease to search them for matches in any other tests. As Table 3-1 indicates, following test 1, the search consistency for the 2-mode case equals 1.00 ($S_{c2} = 1.00$) and the search limits (S_l) have been reduced to 2 modes alone. Note that S_c is the measure of consistency with which a given mode achieves significance in any test. S_c is calculated in this simple example by

$$S_{ci} = t_i / T_i \tag{3-5}$$

where t_i is the number of test-specific data sets within which the i-mode case is found significant and T_i is the number of test-specific data sets in which the i-mode case is included in the search limit list. So far, in this example, $t_2 = 2$ and $T_2 = 2$ giving $S_{c2} = 1.00$. So, when I search through test 2, I find several comparisons where the 2-mode case is significant; thus S_{c2} remains at 1.00. That 3-mode cases are also significant is irrelevant because I have already removed it from the search list. Tests 3 and 4 yield the same results. In tests 5, however, the 2-mode case fails to reach significance at the $\alpha_c = 0.05$ level; thus, the S_{c2} drops to 0.80. The question now arises: what S_c is enough before a mode is excluded from the search limit list (i.e., what is the S_c critical value or $S_{c\,cv}$)? Throughout this paper, I will set the $S_{c\,cv}$ at 0.75—this means that unless a mode appears significant in at least three quarters of the tests, it will be dropped from the search limit list. As I continue to test 6, I once again find that the 2-mode case is significant in each data set. Thus I complete this experiment with $S_{c2} = 0.83$ and conclude that sets *A*, *B*, *C*, and *D* all appear to have 2 modes. However, I don't know yet how this result compares to random cases.

To calculate the significance of this result, I take 1000 groups of the 4 simulated data sets A^1, B^1, C^1, and D^1 through the same experimental search strategy. The results are shown in Fig. 3-10. Note that the *P* value decreases monotonically from 0.242 in the first test: this means that in roughly a quarter of the randomly simulated experiments, some modes are considered significant after 1 test, but, because the search limits are thereafter narrowed, very few simulated experiments give consistent modes. After 6 tests, *P*

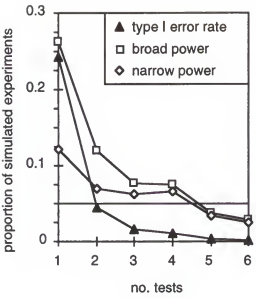

FIG. 3-10. The experiment-wise, type I error rate (*P* value), broad power, and narrow power calculated as the experiment examining sets *A*, *B*, *C*, and *D* proceeds through each of its 6 tests.

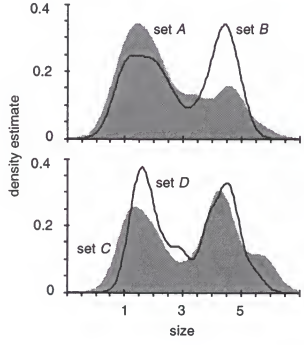

FIG. 3-11. The 2-mode kernel estimates of sets *A*, *B*, *C*, and *D*. Note the high degree of correlation between the modes at this resolution.

reaches 0.001 and is significant at the $\alpha_e = 0.05$ level. Thus, earlier indications that *A*, *B*, *C*, and *D* have 2 modes is found to be a significant result. Fig. 3-11 shows each of sets *A*, *B*, *C*, and *D* with 2 modes.

Also shown in Fig. 3-10 is what I term the broad and narrow power. Power is calculated in LS as the proportion of experiments using simulated data sets sampled from distributions with the same number of modes as the observed data sets. In this example, the test data sets have 2 modes, so 1000 groups of 4 data sets (A^2, B^2, C^2, and D^2), each sampled from 2-mode distributions (created in a similar manner to the 1-mode sampling distributions described earlier) are run through the same experiment. The proportion of experiments finding significant multimodality, including the 2-mode case, is defined as the broad power. The proportion of experiments finding 2 modes exclusively is defined as the narrow power. Fig. 3-10 shows that broad power decreases from 0.262 in test 1 to 0.028 in test 6, while narrow power decreases from 0.121 to 0.025. These power levels are low but are specific to these conditions (i.e., the number of modes, degree of modal definition, sample size, and parameter choice for LS). To get a slightly better idea of the power and behavior of LS, I will now apply it to a variety of conditions.

Power and Behavior

Now I will apply LS to a pair of rather difficult tests. Rather than trying to find 2 modes, I will try to find 10 modes—some of which are poorly defined (Fig. 3-2c). In these examples, I will again use the Eastern North American, boreal-forest, mammal, log body-mass distribution, except I will (1) examine it at the 10-mode resolution rather than 2-mode, and (2) artificially increase the sample size. As was the case for the first example application of

LS, I am not concerned here with what the true number of modes is in this data set; I am simply forcing it to 10 modes and testing whether or not LS can determine this naively. So both examples will have the same 10 modes but the sample size will be increased by a factor of 3 in the first example and by a factor of 6 in the second. In both cases, $S_{c\,cv}$ will be set to 0.75.

Fig. 3-12 shows the type I error rate, broad power, and narrow power for both examples (see Fig. 3-12a for the results when the sample size equals 102 and Fig. 3-12b when it equals 204). When sample size equals 102, broad power reaches 0.310, and at 204, broad power reaches as high as 0.813. Narrow power, however, remains low in both experiments. This should be expected, however, because of the very poor definition of some of the modes. To have so many modes arrayed in such an irregular fashion makes the conditions of these experiments very challenging. It is encouraging that LS, although unable to identify the correct number of modes to the exclusion of all other possibilities, is able to reliably include the correct degree of multimodality in its list of possible cases.

So far I've shown how LS can correctly identify consistent multimodality when it exists. It's important to also know to what degree LS has the tendency to falsely conclude that data sets share the same multimodal structure when none exists. This problem can arise for two reasons: either data sets are unimodal, or they are multimodal but their modes are uncorrelated. I have already seen how LS avoids the first case. In each experiment, LS has calculated the experiment-wise type I error rate (or P value). By definition, this is the probability of finding multimodality in samples from unimodal distributions.

A formal examination of the second case (i.e., the tendency for LS to find consistent multimodality when it is actually uncorrelated) involved a

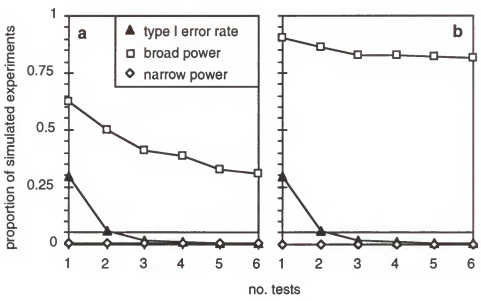

FIG. 3-12. The experiment-wise, type I error rate (*P* value), broad power, and narrow power obtained by the 10-mode experiments. (a) when sample size equals $3n_{NAbm}$, and (b) when sample size equals $6n_{NAbm}$.

series of experiments in which identical bimodal distributions are gradually shifted out-of-phase with each other. These bimodal distributions are the same used in the first example experiment. Fig. 3-2d shows how these distributions appear when they are out-of-phase (i.e., anti-correlated). When completely out-of-phase, one distribution is shifted by 0.5 the distance between the modes (*d*). Four experiments will be conducted using 4 data sets in each. In each experiment, the distributions will be shifted by Δ—a calculated proportion of d. So $\Delta_1 = 0.0625d$ in the first shifting experiment, $\Delta_2 = 0.125d$ in the second, $\Delta_3 = 0.25d$ in the third, and $\Delta_4 = 0.5d$ in the fourth. Sets *A* and *C* are identical to the first example (they are samples from the stationary distribution). To sets *B* and *D* are added one of the proportions (Δ) listed above and are thus denoted as B_Δ and D_Δ. In each experiment, there are

4 tests in the following order: (1) A vs. B_Δ, (2) A vs. D_Δ, (3) C vs. B_Δ, and (4) C vs. D_Δ. The sample size for each data set is again 34.

The significance of the mismatch for all comparisons and tests in each of the 4 experiments is shown in Fig. 3-13. Visually I can see that as these data sets are shifted out-of-phase, different comparisons move in and out of significance. It may seem troubling initially that spurious matching can occur, but I already know that this occurs. Almost any pair of data sets shows some matching as resolution is varied and they are slid past one another. The important features of Fig. 3-13 to note are that spurious matches are isolated to single tests and there is some indication that the total number of matches decreases as the data sets are shifted out-of-phase.

Much more important than a few example experiments, however, is the behavior of LS through many simulated experiments. For each of the 4 degrees of offset, 1000 simulated experiments using sets A^2, B_Δ^2, C^2, and D_Δ^2 (i.e., data sets sampled from 2-mode distributions) were run again using $S_{c\,cv}$ = 0.75 (Fig. 3-14). The probability of finding any modes, the probability of finding modes (including the 2-mode case), and the probability of finding 2 modes exclusively are all calculated from the results of these experiments. These measures show (Fig. 3-14) that as these distributions are shifted out-of-phase, it rapidly becomes exceedingly rare to find any evidence of multimodality. For completeness, the type I error rate was also determined using many data sets simulated from unimodal distributions (sets A^1, B_Δ^1, C^1, and D_Δ^1). As expected, the type I error rate remains low and relatively constant regardless of the degree of phase shifting. It is interesting that the probability of finding any lumps converges with the type I error rate when $\Delta > 0.25d$. This means that LS resists finding multimodality when it is either nonexistent or anti-correlated.

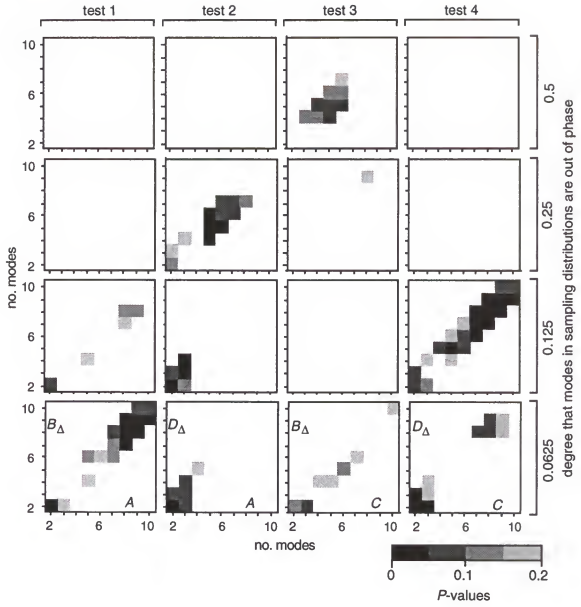

FIG. 3-13. The match significance for all comparisons in all tests in the LS experiments examining sets A, B_Δ, C, and D_Δ. The overall degree of matching generally decreases as sets B_Δ and D_Δ are gradually shifted out-of-phase with A and C. Some spurious significant matching appears but no resolution gives consistent matching across the tests as the shifting proceeds. These results are typical of what occurs over many simulated data sets. This behavior is critical and explains why LS tends not to conclude that multimodality exists when it is either non-existent or uncorrelated.

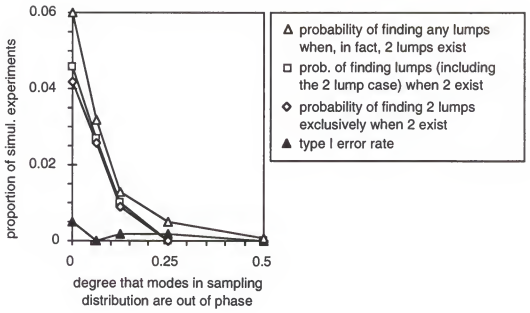
0.06
0.04
0.02
0
proportion of simul. experiments
0
0.25
0.5
degree that modes in sampling distribution are out of phase
Δ probability of finding any lumps when, in fact, 2 lumps exist
□ prob. of finding lumps (including the 2 lump case) when 2 exist
◇ probability of finding 2 lumps exclusively when 2 exist
▲ type I error rate

FIG. 3-14. The experiment-wise, type I error rate (*P* value) and the probability of finding various kinds of multimodality in experiments shifting bimodal distributions out-of-phase.

With the mechanics and behavior of LS now demonstrated, I turn, in the next section, to testing for complex multimodality in ecological data.

Testing for Complex Multimodality in Mammal Body Mass Data

Holling (1992) introduced the Extended Keystone Hypothesis that proposes that over specific scale ranges, natural systems track the behavior of a few controlling factors. Thus metrics of a system's dynamics will fall into specific periodicities, and metrics of a system's structure will fall into specific size groups (or lumps). The more specific Textural Discontinuity Hypothesis predicts that body size distributions will be lumpy as a result of animals employing scale-dependent decisions to exploit resources distributed in a lumpy environment (Holling 1992, Hostetler 1997).

Holling (1992) and Manly (1996) examined the body mass data sets of mammals and birds of the Eastern North American boreal forest and prairie for evidence of multimodality. The two authors agreed that these data sets showed evidence of multimodality, but differed greatly on the number of modes and the strength of evidence in support of their findings. I will attempt to resolve some of this debate through the application of LS. Specifically, I will test mammal body mass data from the boreal regions of Northern Europe, Eastern Russia, and Eastern North America (Fig. 3-15 and Appendix) for any significantly consistent multimodality.

Experimental Design

To test Holling's (1992) Extended Keystone Hypothesis, we must first establish that lumps exist in some general fashion. Data sets large enough to represent well any multimodality they may possess are required. Pooling data helps overcome sampling error, but the danger is that if data sets possess unique multimodality, then pooling will mask their structure. Some efforts to date (Holling 1992, Holling et al. 1996, Restrepo et al. 1997, Lambert and Holling in press) have given weak confirmation of the Extended Keystone Hypothesis and the Textural Discontinuity Hypothesis (Holling 1992) and weak refutation of other lump hypotheses. Therefore, the experimental design will compare the species lists of three regions fitting criteria suitable not only for testing the Extended Keystone Hypothesis, but also the Textural Discontinuity Hypothesis.

Interpreted somewhat conservatively, the Textural Discontinuity Hypothesis (Holling 1992) predicts that animals of the same taxonomic class, gross locomotory style, and habitat should be subject to the same set of ecological forces; therefore, their body mass distributions should have the

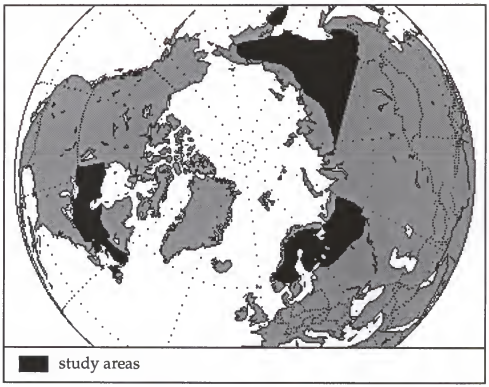

FIG. 3-15. The three boreal forest study areas from which mammal body mass data were collected: Eastern North America, Northern Europe, and Eastern Russia.

same lump structure. Which species should be included in a list is still a matter of interpretation, however, because habitat has no clear definition. At one scale, the boreal forest itself is an identifiable habitat, but at smaller scales, it contains within it a great variety of habitat types. While I will refrain from agonizing over these issues at length, I will assert that it is perhaps best to include only those species that inhabit a specific habitat feature, such as wooded areas dominated by coniferous species. With regard to locomotory style, I will simply exclude bats. Thus, except for the exclusion of two bat species, the Eastern North American boreal mammal data set is the same as that examined by Holling (1992) and Manly (1996). The criteria described above produce comparable data sets for Northern Europe and Eastern Russia.

There are statistical reasons for careful choice of data and interpretation of results in LS. Correlation is not causation. Because two or more data sets have the same multimodal structure does not mean that they are necessarily multimodal. One must have an a priori understanding that each data set is shaped by similar forces. Because I restrict these analyses to animal body mass distributions within the same taxonomic class, gross locomotory style, and habitat, it is reasonable to expect that underlying distributions are at least similar in form—a form determined by the same causative mechanisms.

This boreal mammal LS experiment examines 2-15 modes and consists of 3 tests: (1) Eastern North America (*NAbm*) vs. Northern Europe (*Ebm*), (2) *NAbm* vs. Eastern Russia (*Rbm*), and (3) *Ebm* vs. *Rbm*. The order of tests was arbitrary and decided upon a priori—proceeding from west to east. Unique sampling distributions were calculated for each region from the observed data of that region alone. Thus, the unimodal sampling distribution from which Ebm^1 data sets were simulated, was calculated from the *Ebm* data. Similarly, Rbm^1, $NAbm^1$, data sets were sampled from unique unimodal distributions fit to *Rbm* and *NAbm* respectively. Power must be evaluated in a similar fashion to type I error, so these tests also utilize unique multimodal sampling distributions.

Results

Mismatch significance of each comparison in each test for boreal mammals is shown in Fig. 3-16. It is immediately apparent from Fig. 3-16 that widespread matching exists between these data sets—some of which appears to be consistent throughout all 3 tests. More formally, when I searched for consistent modal structure amongst the tests, I obtained the results shown in Table 3-2. The significance of these results is shown in Fig. 3-17. I found 10-11

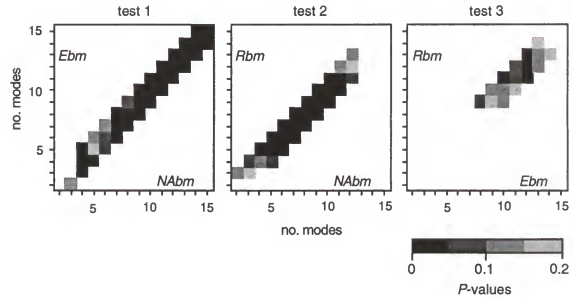

FIG. 3-16. The match significance for all comparisons in all tests in the LS experiment examining the mammals.

TABLE 3-2. Search results obtained by the LS experiment examining boreal forest mammals. A number of multimodal cases show some consistency but the 10 and 11-mode cases emerge as the best candidates.

	test	no. modes: all sets													
	no.	2	3	4	5	6	7	8	9	10	11	12	13	14	15
signif.	1	0	1	2	2	1	2	2	2	2	2	2	2	2	2
count	2	0	0	1	2	0	2	2	2	2	2	0	0	0	0
	3	0	0	0	0	0	0	0	0	1	1	0	0	0	0
search	1	.	0.50	1.00	1.00	0.50	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
consist.	2	.	0.50	0.75	1.00	0.50	1.00	1.00	1.00	1.00	1.00	0.50	0.50	0.50	0.50
(Sc)	3	.	0.50	0.50	0.67	0.50	0.67	0.67	0.67	0.83	0.83	0.50	0.50	0.50	0.50
search	1	.	.	x	x	.	x	x	x	x	x	x	x	x	x
limits	2	.	.	x	x	.	x	x	x	x	x	.	.	.	.
	3	.	.	.	.	.	.	.	.	x	x	.	.	.	.
concl.		.	.	.	.	.	.	.	.	0.83	0.83	.	.	.	.

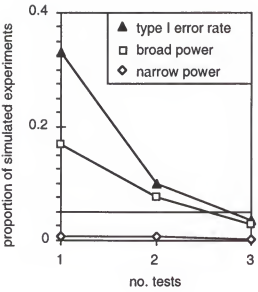

FIG. 3-17. The experiment-wise, type I error rate (P value), broad power, and narrow power obtained by the mammal experiment.

modes in the boreal mammal data sets with an S_{c10} and S_{c11} of 0.83 (P = 0.035). Fig. 3-18 shows the 10-mode kernel estimates of boreal mammals and the corresponding lump and gap intervals.

Discussion

A significant but imperfect match

By eye, there is a high degree of correlation between the three regions in the mammal experiment (Fig. 3-18). The imperfection of this correlation has a number of possible explanations: (1) no multimodality actually exists and apparent correlation (measured or visual) is coincidental, (2) multimodality exists, but at a different resolution for some or all of the data sets, (3) multimodality exists at this resolution, but it is somewhat distinct in each region due to ecological differences, (4) species lists inappropriately

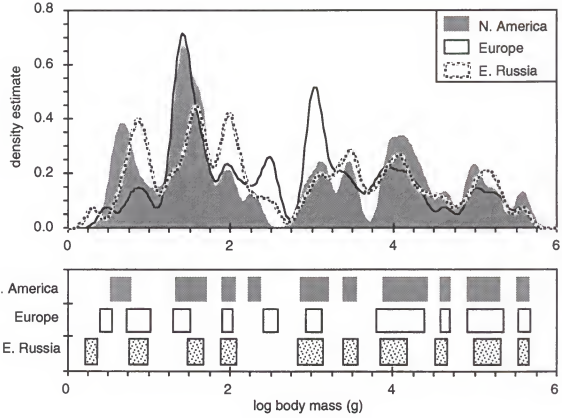

FIG. 3-18. The 10-mode kernel estimates of mammals of Eastern North America, Northern Europe, and Eastern Russia. Also shown are the correspondent lump intervals. Boxed intervals indicate lumps.

include or exclude data, (5) body mass data are inaccurate, and (6) normal kernel estimates, though useful in characterizing local data density, may not be the most natural way to view lumps.

Whenever a test of a novel theory achieves significant results, the natural and appropriate reaction is to be particularly concerned about type I error. Of course, it may have been appropriate to use a lower alpha. When only three regions are examined over many resolutions, however, the only way to achieve very low alpha levels is to set $S_{c\,cv}$ very high. The concomitant sensitivity to test order and loss of statistical power may become too extreme. Alternatively, further tests of the apparent multimodality found

here can be conducted through application of LS to other taxa, regions, and ecological metrics.

Alternatively, imperfect correlation of lump locations shown in Fig. 3-18 may also result from the fact that each data set is a sample of the underlying multimodal distribution. As such, the kernel estimates are actually indicating the location of sample clusters and not the actual hypothesized underlying distribution. It would be useful, then to compare data sets in a manner that permits a greater degree of freedom for each data set to define its modal structure individually. A variation of LS that permits this approach is currently under development.

Imperfect lump correlation can always be explained by the fact that these are not true replicate samples and that each region has a somewhat unique ecology and site history. While there will always be variation that can be accounted for in this way, I am always suspect of "explaining away" differences where similarity is expected. Apparently, the differences are not significant here, however, and this potential problem in interpretation is not an issue. Tests akin to those presented here should produce positive results for Holling's (1992) Extended Keystone Hypothesis or Textural Discontinuity Hypothesis to have general application. If, instead, each community has unique clusters and not general lumps, then the usefulness of this property in providing ecological insight would be greatly hampered.

The issue of whether or not the correct data sets were assembled will probably never be resolved to everyone's satisfaction. The criteria I used to include/exclude data satisfy the requirements of the statistical test and allow the theoretical question to be put at risk.

Problems associated with estimating body mass for each species are another concern. For example, a single mean mass was calculated for each

species and so no account is made here of sexual dimorphism or regional variation. Other potential problems include sample size and seasonal variation. That analysis was conducted on the logarithmic scale helps, but accuracy remains a concern. Consider, however, that data inaccuracies would reduce modal definition, consistency, and thus correlation. That correlation was found at all seems to indicate that the data are accurate enough to permit analysis.

Finally, imperfect lump correlation may partly result from the method used to define modes. Normal kernel estimates give good indications of local data density but other methods (e.g., clustering algorithms) may give more natural aggregations and divisions.

Data sharing

An important factor not yet considered is the degree to which any test's matching results from species appearing in both regions. Consider two species lists taken from adjacent sites with the same habitat—they can have identical data. If so, when these sites are compared in a test, they will give a perfect match at all resolutions (with an equal number of modes). However, matching under such conditions provides little insight. Many species lists, including those used here, share some data (Table 3-3) and thus some of their matching will be due to this factor alone. For example, the Northern European and Eastern Russian data sets share a substantial proportion of their data.

What is needed is some way to mask out the effects of these shared data so that the degree of matching contributed by unique species can be isolated. This is, in fact, what has been done to arrive at the results presented here. To be specific, I have done this in LS by forcing all simulated data sets to include the exact same data points shared by the real sets. For example, *Ebm* and *Rbm*

TABLE 3-3. Shared data (or pairwise set intersection) of boreal forest mammals.

region	n	no. shared data points Europe	E. Russia
N. America	34	8	8
Europe	54	-	31
E. Russia	60	-	-

share 31 data points. In test 3, then, all Ebm^1 and Ebm^9 simulated data sets would consist of those same 31 data points and an additional 23 randomly sampled data points. Similarly, all Rbm^1 and Rbm^9 simulated data sets would consist of those same 31 data points and 29 unique, randomly sampled, data points. In this manner, whatever matching is found in the real sets caused by the shared data is also produced in the simulated sets and thus significance is determined exclusively by the unique data. The only remaining problem is that power is reduced in tests where any substantial proportion of the data are shared. Therefore, matching may exist but the test may be unable to find it significant. There exists, for the moment, no method by which this problem can be remedied other than to choose data sets that share a minimal amount of data.

Although the *Ebm* vs. *Rbm* test gave some significant matching, it is very possible that the loss of power suffered as a result of shared data prevented the detection of other possible lump structures.

Power

The power levels achieved by the mammal experiment are particularly low (Fig. 3-17). This is not surprising, however, because the sample sizes are small, there are many modes, some modes are very poorly defined, some data sets shared a substantial portion of their data, and each sampling distribution

was unique. That I found multimodality at all under these difficult conditions seems to indicate that these data sets are not structured by simple random sampling. From a biological perspective, this is obvious. Body masses are an evolved property—a key feature of any animal affecting its fitness within a given environment. This seems to imply that statistical power of LS is underestimated in these tests. The nonrandom nature of body mass distributions is also discussed by Brown and Nicoletto (1991).

Implications

This experiment was designed to simultaneously test the Extended Keystone Hypothesis and the Textural Discontinuity Hypothesis. The result supports both hypotheses. However, competing hypotheses must be considered because lumps could be caused by factors other than those considered by the Textural Discontinuity Hypothesis.

One hypothesis, the Noah Hypothesis (Holling 1992), is weakened by these results. The Noah Hypothesis is identical to Holling's Urtier Hypothesis, which explains lumps as resulting from historical events (i.e., founder effects and extinction events). It is possible that historical events have limited the number of ancestral forms—leaving some body-size niches unfilled. The Noah Hypothesis thus owes its name to Noah having but few cage sizes. It seems unlikely, given the periods of separation, that each region would still arrive at the same lump structure through the influence of the Noah Hypothesis.

Other hypotheses that are consistent with the results obtained here include: the Limited-Morph Hypothesis (Holling 1992), the Trophic-Trough Hypothesis (Griffiths 1986, Holling 1992), and what I term here the Widespread-Species Hypothesis (Brown 1995). In the briefest terms, the Limited-Morph Hypothesis states that a limited number of life forms (e.g.,

locomotory styles) exist—each of which operate effectively over a narrow range of body masses. The Trophic-Trough Hypothesis states that size-dependent trophic relations initiate and maintain lump structure. Finally, the Widespread-Species Hypothesis proposes that: (1) a few species, or sets of closely related species are widely distributed, and (2) through competitive exclusion and character displacement (acting on body size), these few species affect which other species can coexist (Brown 1995).

LS has identified consistent lumpiness in the boreal forest mammals. Further analysis should now be undertaken to attempt to find convincingly general pattern and sort between these causative hypotheses.

Summary

LS is introduced here as a statistical method well suited to testing for complex multimodality. An LS experiment involves a series of pairwise tests comparing each data set to every other data set over a range of resolutions, and then a search for consistent pattern amongst these tests. For each pair of data sets and each resolution up to an arbitrary limit, the degree of mismatch in the modal structure is calculated. The significance of each of these mismatches is determined by comparing the observed values to those expected from simulated data. Because the significance of each mismatch is evaluated in a comparison-wise manner, a potentially excessive number of data sets will achieve a good match at random through the experiment. To control for the experiment-wise error rate, one must conduct a search for consistent pattern. Consistent pattern in early tests is used to predict pattern in later tests. The search limits are restricted to the resolutions that give a high degree of search consistency.

When LS is applied to data sets that contain very complex multimodality (i.e., many irregularly distributed modes of which some are very poorly defined), it is reasonably capable of including the correct number of modes in its conclusions even if it is limited in its capacity to exclude all other possibilities. LS is thus capable of finding multimodality when it exists but avoids concluding that multimodality exists when it is either uncorrelated or nonexistent.

LS was applied to mammal body mass data sets of the Eastern North American, Northern European, and Eastern Russian boreal forests. Mammals were found to have 10-11 lumps ($P = 0.035$). While these results support Holling's (1986, 1992) assertion that a few cross-scale processes dominate within each ecosystem, further application of LS along with other analyses will be required to find convincingly general pattern and to sort between causative hypotheses. It is unlikely, however, that the lumps found here are the result of the Noah Hypothesis (i.e., historical founder effects and extinction events).

CHAPTER 4
TESTING FOR EVIDENCE OF COMPLEX MULTIMODALITY IN FIRE SIZES AS EVIDENCE OF HIERARCHICAL SYSTEM STRUCTURE IN THE BOREAL FOREST OF MANITOBA, CANADA

Introduction

According to hierarchy theory, ecosystems are structured as a series of scale-specific levels. Each level is defined as a scale range within which factors interact strongly and in relative isolation from other such levels (Allen and Starr 1982, O'Neill et al. 1986). This perspective has been widely regarded as a useful heuristic because it simplifies theoretical system structure. By comparison, traditional concepts of system structure, tend to view individual components of the system as potentially being affected by a great number of processes acting over a great range of scales (Allen and Starr 1982, O'Neill et al. 1986).

Whether ecosystems actually are structured hierarchically, however, is still a controversial issue. Despite this, Holling (1992) proposed a body of theory that simplifies theoretical system structure further by stating that ecosystem structure and dynamics are dominated, over specific scale ranges, by the influence of only a small number of tightly coupled plant, animal, and abiotic processes. The characteristic frequencies at which these processes operate, leave spatial imprints that entrain other processes (Holling 1992). There is a tendency for slowly cycling processes create large structure and rapidly cycling processes create small structure (Holling 1992, Gunderson and Snyder 1994). Because structure is not being created at all scales in between,

the net effect is that metrics of system structure will fall into specific size groups (i.e., frequency distributions will be multimodal; Holling 1992). The question I will address in this chapter is whether or not some specific interpretations of the general theory proposed by Holling (1992) can be applied to fire in the boreal forest of Manitoba.

Wildfire, the Boreal Forest, and Climate Change

Wildfire is a key disturbance agent in the boreal forest and thus strongly influences its distribution, composition, and structure (Heinselman 1973, Johnson 1992, Pastor and Mladenoff 1992, Payette 1992, Sirois 1992, Stocks 1993, Kuhry 1994, Lavoie and Payette 1996). Within the mid-continental boreal forest of North America, wildfire has a particularly dominant effect (Heinselman 1973, Stocks and Street 1983, Suffling et al. 1988, Ehnes and Shay 1995, Suffling 1995). At large scales, climate constrains fire regime. Local conditions determine whether point ignitions either self-extinguish or propagate from stand to stand to cover up to thousands of square kilometers.

The present assessment of potential global climate change projects an increase in temperature and a possible increase in precipitation in mid-continental North America (Boer et al. 1992, Watson et al. 1995). The predicted net effect is a substantial decrease in summer soil moisture (Manabe and Wetherald 1986, Singh and Wheaton 1991, Boer et al. 1992, Watson et al. 1995). A number of authors predict dramatic increases in fire occurrence and subsequent distribution, composition, and structural changes in the boreal forest as a result (Overpeck et al. 1990, Wein 1990, Flannigan and Van Wagner 1991, Stocks 1993, Wotton and Flannigan 1993, Hogg and Hurdle 1995). Anticipating the response of the boreal forest to predicted climate change,

however, would benefit by an improved understanding of fundamental ecosystem processes (Watson et al. 1995, Stocks 1993). Considering the present dominant effect fire has on the mid-continental boreal forest and the potentially dramatic increase in its occurrence with climate change, an improved understanding of fire would be key to projecting future conditions.

Holling (1980, 1986, 1987, 1992) argued that ecosystems can be shifted amongst multiple stable states. The periodic cycling of just a few key processes (e.g., succession of particular plant species following fire) defines the present stable state (Holling 1992). Different patches of the landscape may be in different stages of succession, but the landscape as a whole maintains a stable state as a shifting mosaic. With sufficient perturbation, however, the system can stop tracking the periodic cycling of one or more of these key processes and rapidly shift into a very different stable state (Holling 1992). Considering the potentially profound effect that climate change is predicted to have on fire and the boreal forest, it is useful to know whether the fire regime might shift in a punctuated style from one stable state to a very different one, or in a graded fashion between many possible states.

Mechanisms Underlying Hierarchical System Structure in the Mid-Continental Boreal Forest—Evidence and Alternatives

Considering the important role fire plays in the mid-continental boreal forest, it must feature prominently in any theoretical explanation of how this system operates. The general body of theory proposed by Holling (1992) seems as though it could be interpreted to apply in two ways. It is possible that fire is just one of a number of plant, animal, and abiotic structuring processes. Characteristic sizes of forest patches are created by the distinct periodicities over which these processes operate. Taken together, they create a multimodal

distribution of patch sizes in the forest. Alternatively, it is possible that fire itself is controlled by a small number of factors that operate at distinct periodicities and create multiple modes in the distribution of fire sizes. The latter interpretation is the one that I will test in this chapter but before I do this I will describe it in more detail by invoking several possible mechanisms.

In chapter 2, I proposed an interpretation of the general body of theory that Holling (1980, 1986, 1987, 1992) advocated. Specifically, I proposed that fire size is a function of fluctuating climatic conditions and the slow accumulation of fuel as each stand ages. Fires tend to be small until enough fuel has accumulated and climatic conditions favor fire. When conditions are favorable, a threshold is crossed and many large fires occur. Over time, a multimodal distribution of fire sizes results. Cycles associated with fuel accumulation and climate would be marked by the periodic return of large fires (see also Clark 1988, 1989, 1990a, 1990b). However, I have demonstrated that in the case of wildfire in the mid-continental boreal forest, stand age is unrelated to burn hazard and so multimodality cannot occur in fire sizes in this manner—that is, at least under the range of climatic conditions experienced through the mid-twentieth century (see chapter 2). Despite this result, other mechanisms may have been at work.

Climate is well understood to have a controlling influence on wildfire (Flannigan and Harrington 1986, 1988, Clark 1988, 1989, 1990a, 1990b, Hirsch 1989, Payette et al. 1989, Johnson 1992, Johnson and Wowchuk 1993, Stocks 1993, Hogg 1994, Kuhry 1994, Bessie and Johnson 1995, Larsen and MacDonald 1995, Lavoie and Payette 1996). If a few climatic phenomena control fire and they occur at distinct periodicities and spatial extents, then their interaction may produce a multimodal distribution of fire sizes. For example, Gunderson and Snyder (1994) found evidence that 6-7 month, annual, and 10-

14 yr cycles in fire occurrence were associated with climatic factors in the Everglades. They also found suggestive evidence for multimodality in fire sizes although the method they used is probably of limited value (Cox 1966, Silverman 1986). Despite this, Gunderson and Snyder (1994) suggested that small fires were associated with rapidly cycling climatic phenomena and large fires with slowly cycling climatic phenomena. The long-term phenomena tend to act over large areas and short-term phenomena tend to act over small areas (Gunderson and Snyder 1994).

In another example, Johnson and Wowchuk (1993) used an informal technique to identify two possible modes in distributions of total annual area burned in the southern Canadian Rocky Mountains. Johnson and Wowchuk (1993) invoke a climatic mechanism to explain this pattern. Over most the length of the fire season, there is a slow, steady increase in the mean daily Drought Code. The Drought Code is defined as the component of the Canadian Forest Fire Weather Index System (Van Wagner 1988) that relates dryness of the deep compact layer of organic matter to daily atmospheric temperature, humidity, and precipitation. Episodic shifting of the jet stream positions high-pressure systems over the forest and dries fuels over large areas for periods of days to weeks (Daley 1991, Johnson 1992, Johnson and Wowchuk 1993). In some years, the high-pressure system tends to be positioned over the southern Canadian Rocky Mountains early in the fire season, while other years, this doesn't tend to occur until much later in the fire season. Johnson and Wowchuk (1993) found that the timing of the shifting of the high-pressure systems in combination with the slow, season-long increase in mean daily Drought Code tends to constrain the total area burned in their study areas to one of two categories. The four adjacent study areas in the Southern Canadian Rockies ranged between 1300 and 1400 km^2.

Early season occurrence of the high pressure system over the region tended to give a total area burned of <(10-25) ha, whereas late season occurrence tended to burn ≥(10-25) ha (Johnson and Wowchuk 1993). The episodic positioning of high pressure systems has also been noted to be associated with large burn area in the boreal forest more generally (Flannigan and Harrington 1986, Johnson 1992).

Another simple mechanism that may complicate the fire size distribution is the critical percolation threshold (von Niessen and Blumen 1988, Turner et al. 1989, Peterson 1994, Turner and Romme 1994, Gardner and O'Neill 1991, Ratz 1995). Consider a landscape throughout which the burn hazard varies locally to create a patchwork of burnable sites separated by non-burnable sites. Well below the critical percolation threshold, not enough burnable sites are adjacent to each other (i.e., too many sites have a low burn hazard) and fires tend to rapidly self-extinguish. When climatic conditions are favorable, enough burnable sites are adjacent (i.e., enough sites have a high burn hazard) and fires tend to propagate from site to site across the landscape. The critical percolation threshold is defined as the minimum density of burnable sites to create a single connected patch from one end of the study area to the other (Turner et al. 1989). So, as the connectivity increases linearly, we should get incrementally larger fires, but near the percolation threshold, fire sizes increase rapidly and a dip in the fire size distribution may result (i.e., we get two modes).

Whether the theoretical mechanisms described above or some other simple mechanism is controlling fire, a multimodal distribution of fire sizes is difficult to explain outside the context of Holling's (1992) theoretical proposal. I have developed Lump Simulation (LS) as a new statistical method well suited to test for complex multimodality (see chapter 3). I will

apply LS here to fire size distributions of the Manitoban boreal forest as a partial test of whether the boreal forest is hierarchically structured in the manner that Holling (1992) suggests. I will also characterize the general fire regime within subregions of Manitoba.

Study Site

The chosen study site was the province of Manitoba, Canada (Fig. 4-1). Manitoban ecoclimatic regions (i.e., regions of similar climate as defined by distinct plant associations) range from the low arctic through boreal to transitional grassland (Ecoregions Working Group 1989; Fig. 4-2). Analysis focused primarily on the subhumid mid and high-boreal regions. These regions are dominated by Canadian Shield topography, which contains a great many rivers and lakes; notably included are some very large water bodies such as L. Winnipeg. In the mid-boreal, the mineral soils of upland areas are dominated by jack pine (Pinus banksiana), but include white spruce (Picea glauca), trembling aspen (Populus tremuloides), paper birch (Betula papyrifera), and balsam fir (Abies balsamea; Woo et al. 1977, Dutchak et al. 1978). In the high-boreal region, jack pine is less dominant on drier sites, which also include black spruce (Picea mariana), white spruce, trembling aspen, balsam fir, and paper birch. Throughout the boreal forest, moss and lichen spp. are widespread. The often thick organic soils of lowland areas are dominated by sphagnum moss (Sphagnum spp.), black spruce, and tamarack (Larix laricina; Woo et al. 1977, Dutchak et al. 1978). Colder, wetter sites are occupied by bogs and fens (Woo et al. 1977, Dutchak et al. 1978). Wildfire interrupts successional progression and direct species replacement is typical.

Fire is by far the dominant disturbance process within the study region. Manitoba Natural Resources (1986, 1991) indicates that of all stand-replacing

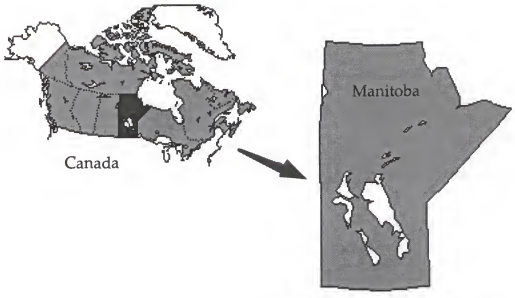

FIG. 4-1. The location of the study area: Manitoba, Canada.

disturbance, 92% is caused by fire, 4% is due to logging, and 4% is due to insect defoliation. The degree and distribution of fire protection is complex, but there is a general decrease from south to north. Aside from buildings and private property, it is likely that fire protection has had limited effect within the mid and high-boreal regions (Glenn Peterson, personal communication). Because fire protection has a much greater effect in the south of the province, the low-boreal regions were not included as part of the study area for the main analysis. The subarctic and arctic regions were excluded because fire occurrence becomes rare that far north.

A few small towns and Indian Reservations are scattered throughout the very sparsely populated study area. A few transportation routes thread through the region. A number of large provincial parks, within which fires are managed, are located along the western edge of Manitoba, generally within the mid-boreal ecoclimatic region. Atikaki Provincial Park, located on

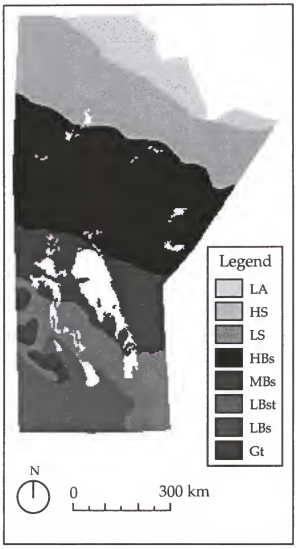

FIG. 4-2. Ecoclimatic regions of Manitoba: low arctic (LA), high subarctic (HS), low subarctic (LS), subhumid high-boreal (HBs), subhumid mid-boreal (MBs), subhumid low-boreal transitional (LBst), subhumid low-boreal (LBs), and transitional grassland (Gt) (from Ecoregions Working Group 1989). Fire size distributions are tested for multimodality within the high-boreal and mid-boreal regions only.

the eastern edge of Manitoba is an exception in that fires are not managed within its boundaries.

Methods

Digitization, Mapping, and General Characterization of Data

Digitization of a map of ecoclimatic regions. I digitized a map specifying the ecoclimatic zones of Manitoba into the Map II® Geographic Information System (GIS). More specifically, using a light table, I traced a paper map of ecoclimatic regions (Ecoregions Working Group 1989) onto blank paper. Major coordinates were also marked to enable later use of GIS rubber-sheeting of the image onto the Universal Transverse Mercator (UTM) map-projection. This image was digitized using an AppleScan® scanner at 300 dpi. A paint program (UltraPaint™) was used to clean up the scanned images and paint each ecoclimatic region a different color. This image was then imported into the Map II® GIS. The digital image was then converted into a map by rubber-sheeting. A majority-scan and a manual check was performed to reduce remaining distortions. The final digitized map was accurate to 4 km^2 (2 km on a side).

Mapping wildfire. I obtained monthly fire records covering the entire province for the years 1976 through 1991 from Manitoba Natural Resources (Manitoba Natural Resources: Forestry Branch, Forest Health and Ecology, Box 70, 200 Saulteaux Crescent, Winnipeg, Manitoba R3J-3W3). Before any work could be done with these data, I removed as many errors as possible. Each fire was recorded as point data, the location of which was specified by region, district, management unit, township, and range. The most precise location (accurate to approximately 10 km) is specified by township and range and so these were used as map coordinates. I converted the text data file

given by Manitoba Natural Resources into a Microsoft Excel® spreadsheet database. The fire records were then imported as point data into the Map II® GIS. Through coloring each subgroup in the database according to region, district, and management unit, I was able to identify consistent errors. A principle meridian runs N-S through the center of the province. Most of the errors in the location of fires were the result of the range specifying the wrong side this meridian. The magnitude of the range was correct, it was just that it specified the wrong direction. To remove this problem, I assumed the region, district, and management unit were correct and re-assigned the fire to the opposite side of the principle meridian accordingly. Errors of unknown origin remained, however, and so these data were omitted from all further analyses except two metrics of the general fire regime (see below). Of an original 13,196 fires, I was able to place 10755 accurately. These fires were then mapped into the ecoclimatic regions.

Measures of fire regime. I calculated the fire cycle, mean fire size, and fire density for each ecoclimatic region. The fire cycle simply measures the number of years required to burn just once an area equivalent in size to each ecoclimatic region. I calculated the total area burned annually and fire-impact distribution in the high and mid-boreal regions. Note that fire-impact simply measures the cumulative proportion of all area burned by fires of increasing size.

For the most part, all fires considered to occur in Manitoba (1976-1991) and reported in this chapter, are the 81.5% that could be mapped accurately. However, the calculated fire cycles will be overestimated and fire density will be underestimated unless all the data are included. I attempted to correct for the missing data by simply assuming that they are distributed within each ecoclimatic region in exactly the same proportion as the accurately mapped

data. Similarly, I assumed that the distribution of fire sizes in the remaining data is the same as that found in the accurately mapped data. Thus, in the case of fire cycle (F), a corrected value (F')can be found by

$$F' = F \times 0.815 \tag{4-1}$$

and in the case of fire density (D), a corrected value (D') can be found by

$$D' = D/0.815. \tag{4-2}$$

Testing for Multimodality in Fire Sizes

To test for complex multimodality in fire sizes, I applied Lump Simulation (LS)—a method I developed and describe in chapter 3. Briefly, the approach LS takes is to search for sample clusters that consistently occur in the same location amongst 3 or more data sets. Data sets are examined in this way at a number of resolutions (i.e., 2 through k clusters or modes, where $2 \leq k \leq 20$). An index is derived that measures the degree of correlation between modes. Multimodality is found if the degree of correlation exceeds that expected from data sets sampled from unimodal null distributions.

When testing for pattern, one should maximize statistical power while maintaining a low type I error rate. In the case of LS, greater statistical power is achieved when more data sets are included in the analysis, but two limits are reached: (1) care must be taken to only include data sets shaped by the same forces, and (2) computation time grows geometrically with the number of data sets compared. Therefore, I attempted to identify groups of up to 6 data sets that seemed to qualify as repeat samples. I summed the total area

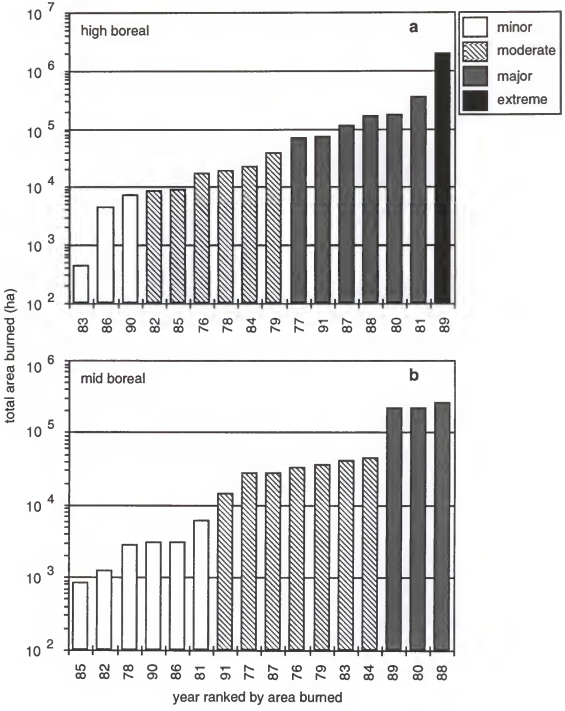

FIG. 4-3. The total area burned annually within: (a) the high-boreal, and (b) the mid-boreal ecoclimatic regions of Manitoba (1976-1991: including the accurately mapped data only). Indicated are the four experimental groups of data sets that were compared for consistent multimodality using Lump Simulation: high-boreal major, high-boreal moderate, mid-boreal major, and mid-boreal moderate fire-years.

burned each year in each ecoclimatic region. Proceeding carefully, I assumed for the moment that years with very different totals may be influenced by different factors. As such, I separated the data into subgroups by the total area burned annually (Fig. 4-3). In the high-boreal, the area burned in 1989 is nearly than twice that burned in all other years combined (Fig 4-3a). As such, it was excluded from further LS analysis. The 6 next most fire-prone years 1981, 1980, 1988, 1987, 1991, and 1977 formed the high-boreal major fire-year group and were compared to each other. Three other groups were formed (i.e., high-boreal moderate, mid-boreal major, and mid-boreal moderate fire-year groups) as shown in Fig. 4-3a and b. The minor fire-years from each region were omitted because of their small sample sizes. Major fire-year groups were tested for 2-15 modes and moderate fire-year groups were tested for 2-12 modes. A maximum of 12 modes was examined in the moderate fire-year groups because sample sizes were more limiting than in the case of major fire-year groups. I excluded all fires <10 ha because visual assessment of their distributions seemed to indicate they were affected by rounding error and also because LS cannot proceed efficiently with large data sets.

The power of the LS tests was also maximized by varying two parameters: comparison-wise alpha level (α_c), and critical search consistency (S_c). At a specific resolution, these parameters govern how well a single pair of data sets must match each other and the degree of consistency that must be achieved between all data sets (see chapter 3). More specifically, at each resolution (i.e., number of modes), each data set is paired against every other. It is not necessary for a single pairwise test to match significantly at an alpha level of 0.05 (i.e., a comparison-wise alpha level = 0.05). It's also not important for every single pairwise test to give a significant match at a specific resolution (i.e., a critical search consistency = 1.0). These parameters can be

varied so long as the probability that sufficiently consistent matching occurs relatively rarely among data sets simulated from unimodal null distributions. In other words, the experiment-wise error rate (α_e) must be kept low. In these LS experiments, each group of data sets was tested using two parameter combinations: (1) $\alpha_c = 0.05$ and $S_c = 0.20$, and (2) $\alpha_c = 0.10$ and $S_c = 0.33$. In the first combination, a highly significant match must be found but only in 20% of all pairwise tests, and in the second, a less significant match must be found in only 33% of all pairwise tests.

Results

General Fire Regime

From North to South, a generally decreasing trend in mean fire size can be seen in Fig. 4-4a. Also from North to South, a generally increasing trend in fire density can be seen in Fig. 4-4b. No clear trend can be seen in fire cycle. In the low subarctic, the fire cycle is 240 yr and within the boreal regions, it varies between 77 and 170 yr. Although general fire regime indices for the transitional grassland are not shown in Fig 4-4, the mean size of 123 accurately mapped fires was 457 ha. Corrected estimates of fire density and fire cycle come to 1.48 fires/(10^4 km^2 yr) and 1476 yr respectively for the transitional grassland. Fig. 4-4 does not show the fire regime for the low arctic or high subarctic ecoclimatic regions because the sample size is so low in those regions (i.e., 0 and 3 respectively).

Great annual variability in total area burned in the high and mid-boreal regions is demonstrated in Fig. 4-3. A few years account for most of the area burned. In the high-boreal, for example, the area burned in 1989 nearly doubles that burned in all other years combined.

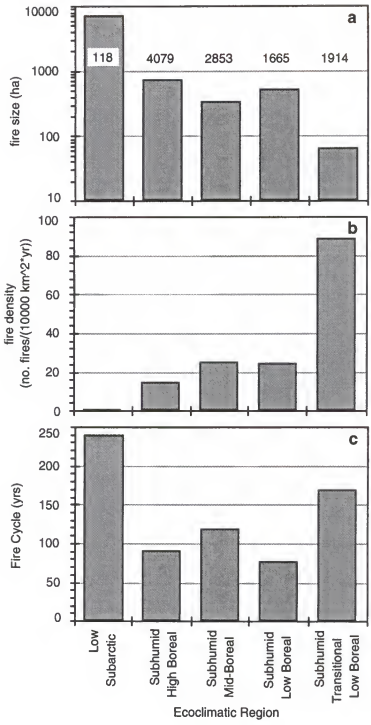

FIG. 4-4. Three metrics of fire regime calculated over 1976-1991 within each ecoclimatic region of Manitoba: (a) mean fire size, (b) fire density, and (c) fire cycle. Note that fire cycle and fire density are corrected estimates that make use of both accurately and inaccurately mapped data. The sample size of the accurately mapped data within each region is also indicated in (a).

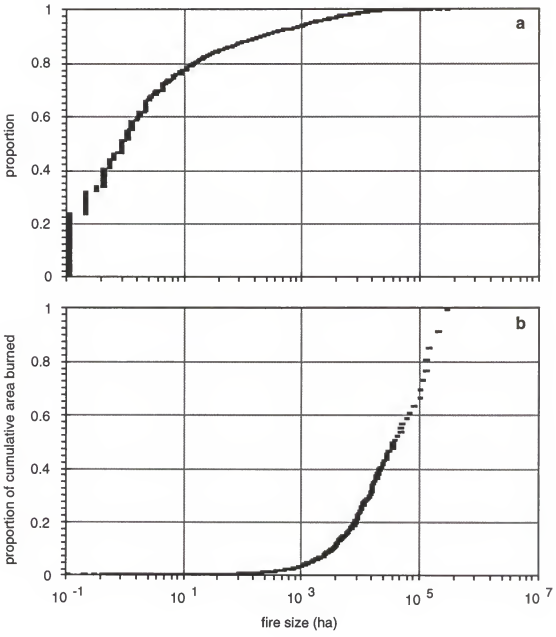

FIG. 4-5. Distributions of all accurately mapped fires occurring between 1976 and 1991 in the Manitoban high-boreal ecoclimatic region: (a) the cumulative frequency distribution, and (b) fire-impact distribution. Fire-impact indicates the cumulative proportion of the total area burned by fires of increasing size.

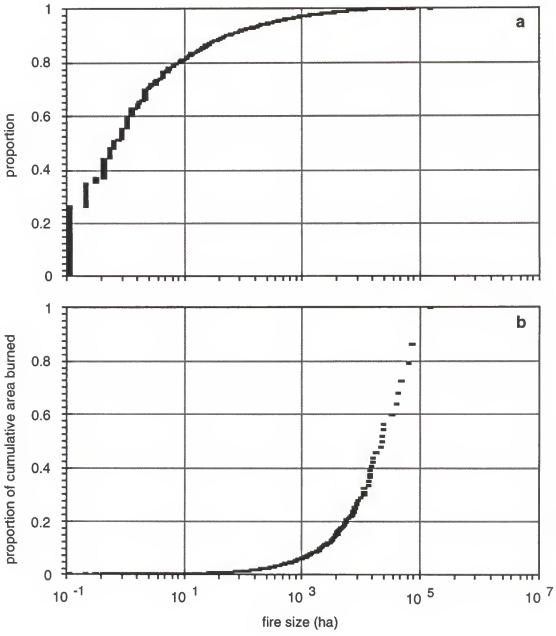

FIG. 4-6. Distributions of all accurately mapped fires occurring between 1976 and 1991 in the Manitoban mid-boreal ecoclimatic region: (a) the cumulative frequency distribution, and (b) fire-impact distribution. Fire-impact indicates the cumulative proportion of the total area burned by fires of increasing size.

Table 4-1. Results of Lump Simulation experiments.

experimental data set group	mean sample size*	no. data sets	no. modes tested	comparison-wise alpha	critical search consistency	modes found
high-boreal major	73	6	2-15	0.05	0.20	—
				0.10	0.33	—
high-boreal moderate	34	6	2-12	0.05	0.20	—
				0.10	0.33	—
mid-boreal major	73	3	2-15	0.05	0.20	—
				0.10	0.33	—
mid-boreal moderate	34	6	2-12	0.05	0.20	—
				0.10	0.33	—

* mean sample size of each data set in the group

Visual inspection of the distributions of all accurately mapped fires occurring in the high and mid-boreal regions (1976-1991) indicates a few data clusters and thus the possibility of multimodality (Fig. 4-5 and Fig. 4-6). The left side of the cumulative frequency distributions (Fig. 4-5a and Fig. 4-6a) have a "staircase" pattern, but this is simply the result of rounding error. However, the right side of the fire-impact distributions (Fig. 4-5b and Fig. 4-6b) indicates a few clusters containing a small number of large fires. Fig. 4-5 and Fig. 4-6 also indicate that although many small fires occur, they account for a very small proportion of all area burned. In the high-boreal <4% and <0.1% of the total area burned is contributed by fires <1000 ha and <10 ha in size

respectively. In the mid-boreal <6% and <0.3% of the total area burned is contributed by fires <1000 ha and <10 ha in size respectively. On the extreme right side of the distributions, >40% of the total area burned is contributed by 10 fires in the high-boreal and 6 fires in the mid-boreal. It is also notable that all of the 10 largest fires in the high-boreal occur in 1989 and 1981—the years in which the greatest total area burned (Fig. 4-3). The 6 largest fires in the mid-boreal occur in 1980, 1988, and 1989; again, these are the years in which the greatest total area burned in that region (Fig. 4-3).

Tests for Multimodality in Fire Sizes

The results of the LS analysis are shown in Table 4-1. In no experiment was any multimodality found in fires ≥10 ha in size at an experiment-wise alpha level of 0.05.

Discussion

General Fire Regime

Fig. 4-4 indicates the important effect of climate on wildfire at the regional scale. Generally, from North to South, fire size decreases and fire density increases. Similar trends have been noted for the province of Ontario by Stocks (1983). The fire cycle is 240 yr in the low subarctic and varies between 77 and 170 yr within the boreal ecoclimatic regions. It seems likely that the changes in fire regime between ecoclimatic regions follow a gradient rather than thresholds corresponding to regional ecoclimatic boundaries (Payette et al. 1989, Stocks 1983). Accurate characterization of the fire regime could not be accomplished in the low arctic and high subarctic because sample

sizes were very small. The transitional grassland has been converted to farmland and, as such, the natural fire regime cannot be determined there.

It is clear that large fires have an overwhelming impact upon the boreal forest (Figs. 4-5 and 4-6). Despite many small fires occurring, the total area they burn sums to a very small proportion. A small number of very large fires account for much of the total area burned (Figs. 4-5, 4-6) and occur during years of greatest total area burned (Fig. 4-3). These trends seem to confirm the findings of other authors regarding the important influence that climate has on wildfire. Exactly which climatic factor is important is not investigated here but has been examined elsewhere (Flannigan and Harrington 1986, 1988, Clark 1988, 1989, 1990a, 1990b, Flannigan and Van Wagner 1991, Hirsch 1991, Johnson and Larsen 1991, Johnson 1992, Johnson and Wowchuk 1993, Wotton and Flannigan 1993, Hogg 1994, Bessie and Johnson 1995, Larsen and MacDonald 1995).

Multimodality and Theoretical System Structure of the Mid-Continental Boreal Forest

Lump Simulation clearly demonstrated that the distributions of fire sizes are not multimodal (Table 4-1). The irregularities at the upper end of the distributions shown in Figs. 4-5b and 4-6b are therefore simply the result of sampling error (i.e., few fires reach extreme sizes). Fires <10 ha in size were not included in the LS analyses, but are shown in Figs. 4-5a and 4-6a. Although rounding error prevents firm conclusions, it seems likely that very small fires fall into the same continuous distribution as larger fires. Therefore, I conclude that fires reach arbitrary sizes in a continuous distribution.

As discussed earlier, a discontinuous distribution of object sizes in the landscape is argued as evidence of scale-specific processes producing scale-specific structure. For example, Kent and Wong (1982) measured the length of lake shorelines with varying stick-lengths and calculated the fractal index. They attributed a break in the fractal index distribution to a transition from large structure produced by glacial processes to much smaller structure produced by erosion. Tests for multimodality and fractal analysis accomplish similar ends. An advantage LS offers, however, is an objective determination of the location of discontinuities. It may still be possible that direct measures of stand structure rather than fire sizes may possess multimodal distributions or fractal breaks (Kent and Wong 1982, Krummel et al. 1987, Milne 1988, Palmer 1988, De Cola 1989, O'Neill et al. 1991, Leduc et al. 1994). Further investigation into this question would provide independent tests of whether the mid-continental boreal forest is structured hierarchically. It may be particularly productive to include in such tests smaller scales than those examined here. The conclusions I come to here, however, will be based on the somewhat limited scope of evidence given by the metrics of wildfire I examined over landscape and regional scales.

Because no multimodality exists in the distribution of fire sizes, I have found no supporting evidence that a few, highly periodic, cross-scale factors control wildfire in the boreal forest. On the contrary, it seems that the factors that control wildfire seem to be many in number and/or highly stochastic. Whenever many factors have a small effect on a system, then metrics of system structure tend to fall into continuous distributions. Similar results are achieved even if a small number of factors controlling a system, provided their effects are complex and subtle. For example, the turbulent effect of wind

can change the intensity, direction of propagation, and eventual size of a fire through the complex net impact of many momentary gusts.

The lack of multimodality also suggests that no hierarchical scale breaks occur over the range of scales examined. That is, because fire falls into a continuum of sizes, there seems to be no transition where different sets of factors control fire over specific scale ranges.

If, as these results suggest, many and/or highly stochastic factors control wildfire in the boreal forest and no scale breaks occur over a wide range of scales, there are important implications for prediction, modeling, and response to climate change. For example, qualitative fire dynamics can be easily emulated with a simple, stochastic, spatial-percolation model over the wide scale range examined here. However, fire behavior or the eventual size reached by any given fire will be difficult phenomena to assess because computer models rapidly reach practical limits as degrees of complexity are added.

Possible climate change is predicted to increase fire occurrence. The impact on the boreal forest depends, in part, on whether the fire regime shifts in a punctuated style from one stable state to a very different one (Holling 1980, 1986, 1987, 1992), or in a graded fashion between many possible states. My results suggest the latter. Each fire occurs within slightly different climatic, topographic, and vegetative conditions. As a result, each fire reaches a specific size within an overall continuum. At least up to some limit, a graded shift to climatic conditions that increase fire occurrence should simply increase the size of individual fires and produce an upward displacement in the overall fire size distribution. That is not to say that incrementally increased fire occurrence cannot elicit threshold responses in the fire regime and the ecosystem in general. The boreal forest is not floristically diverse, and

if fire occurs too often over wide areas, some species will be unable to regenerate sufficiently and will become locally extinct. The direct physiological effects of climate on plants can have similar effects. The effect that exclusion of plant species can have on the system may be marginal or profound. A distinct, yet boreal forest may persist, or large areas may convert to grassland.

All of these conclusions are valid within the context of the range of climatic conditions occurring in Manitoba between 1976 and 1991. With a substantial increase in atmospheric CO_2, global circulation models predict higher temperatures with a high degree of confidence, but predict regional precipitation with lower confidence (Boer et al. 1992, Watson et al. 1995). Under unique climatic conditions, it is not possible to accurately predict system behavior. If, however, potential climate change is characterized by an increased frequency of the kind of extreme fire years we already have seen, then we can simply expect to see proportionally larger fires. Contrary to the originating hypothesis of this study, these increases will fall into an open ended continuum rather than any predictable set of categories.

Conclusions

Regional trends in fire regime suggest that climate has an important effect on boreal forest wildfire. From North to South, fire size decreases, and fire density increases. Fire cycle also varies between ecoclimatic regions. Also, the total area burned in the boreal forest is largely accomplished by very large fires that seem to be occurring during extreme fire years.

Lump Simulation clearly demonstrated that the distribution of fire sizes in the boreal forest is not multimodal. Therefore, the factors that control wildfire seem to be many in number and/or highly stochastic.

Furthermore, no hierarchical scale breaks seem to occur over the range of scales examined.

Therefore, qualitative fire dynamics can be easily emulated with a simple stochastic spatial-percolation model over a wide range of scales. Prediction of fire behavior, however, will likely prove to be a difficult task. Insofar as potential climate change creates conditions similar to extreme fire years of the past, we can expect an upward displacement of the continuous fire size distribution. Of concern is the possible increase in frequency of extreme conditions such as occurred in Manitoba in 1989 where 5.7% of the entire province burned (Hirsch 1991).

APPENDIX
MAMMALS OF THE BOREAL FOREST* †

scientific name	common name	mass (g)	log mass (g)	NAbm	Ebm	Rbm
Ovis canadensis	Bighorn Sheep	108000	5.0334	.	.	x
Alces alces	Elk	373750	5.5726	x	x	x
Capreolus capreolus	Roe Deer	23025	4.3622	.	x	x
Cervus elaphus	Red Deer	131620	5.1193	.	x	x
Odocoileus virginianus	White-Tailed Deer	86409	4.9366	x	x	.
Rangifer tarandus caribou	Woodland Caribou	105687	5.0240	x	x	x
Moschus moschiferus	Musk Deer	13500	4.1303	.	.	x
Sus scrofa	Wild Boar	154875	5.1900	.	.	x
Alopex lagopus	Arctic Fox	3450	3.5378	.	x	x
Canis latrans	Coyote	14061	4.1480	x	.	.
Canis lupus	Wolf	42850	4.6320	x	x	x
Cuon alpinus	Dhole	11500	4.0607	.	.	x
Nyctereutes procyonoides	Raccoon Dog	6750	3.8293	.	x	x
Vulpes vulpes	Red Fox	5194	3.7155	.	x	x
Felis bengalensis	Leopard Cat	2700	3.4314	.	.	x
Lynx lynx	Lynx	17800	4.2504	x	x	x
Panthera pardus	Leopard	32000	4.5052	.	.	x
Gulo gulo	Wolverine	12304	4.0900	x	x	x
Lutra canadensis	River Otter	9072	3.9577	x	.	.
Lutra lutra	Otter	8175	3.9125	.	x	x
Martes americana	Marten	839	2.9238	x	.	.
Martes flavigula	Yellow-Throated Marten	2000	3.3010	.	.	x
Martes foina	Beech Marten	1000	3.0000	.	x	.
Martes martes	Pine Marten	1380	3.1399	.	x	.
Martes pennanti	Fisher	3118	3.4939	x	.	.

* All non-volant species are included that inhabit coniferous dominated forested areas, although the N. American list also includes species from mixed conifer-deciduous areas.

† Geographic range data were compiled from Corbet (1978) for eastern Russia (Rbm) and from Van Den Brink (1968) for Europe (Ebm). Mass data was collected from Silva and Downing (1995). Holling (1992) was consulted for all N. American data (NAbm).

scientific name	common name	mass (g)	log mass (g)	NAbm	Ebm	Rbm
Martes zibellina	Sable	1380	3.1399	.	.	x
Meles meles	Badger	9220	3.9647	.	x	x
Mephitis mephitis	Striped Skunk	2642	3.4220	x	.	.
Mustela altaica	Mountain Weasel	127	2.1038	.	.	x
Mustela erminea	Ermine	81	1.9074	x	x	x
Mustela eversmanni	Steppe Polecat	1043	3.0184	.	x	.
Mustela lutreola	European Mink	1182	3.0725	.	x	.
Mustela nivalis	Least Weasel	45	1.6484	x	x	x
Mustela putorius	Polecat	899	2.9540	.	x	.
Mustela sibirica	Siberian Weasel	1250	3.0969	.	x	x
Mustela vison	Mink	1225	3.0880	x	.	.
Selenarctos thibetanus	Asiatic Black Bear	70000	4.8451	.	.	x
Ursus americanus	Black Bear	169643	5.2295	x	.	.
Ursus arctos	Brown Bear	204500	5.3107	.	x	x
Erinaceus europaeus	Hedgehog	1019	3.0082	.	x	.
Blarina brevicauda	Short-Tailed Shrew	25	1.3896	x	.	.
Microsorex hoyi	Pygmy Shrew	4	0.6138	x	.	.
Neomys fodiens	Water Shrew	16	1.2041	.	.	x
Sorex araneus	Common Shrew	7	0.8692	.	x	x
Sorex arcticus	Arctic Shrew	7	0.8692	.	.	x
Sorex cinereus	Common Shrew	5	0.7197	x	.	x
Sorex daphaenodon	Large-Toothed Shrew	7	0.8319	.	.	x
Sorex dispar	Gray Long-Tailed Shrew	6	0.7404	x	.	.
Sorex fumeus	Smoky Shrew	8	0.9224	x	.	.
Sorex gaspensis	Gaspe Shrew	4	0.5664	x	.	.
Sorex gracillimus	Slender Shrew	4	0.6021	.	.	x
Sorex minutissimus	Least Siberian Shrew	2	0.3010	.	.	x
Sorex minutus	Pygmy Shrew	3	0.4771	.	x	.
Sorex palustris	Water Shrew	13	1.1200	x	.	.
Sorex sinalis	Dusky Shrew	7	0.8692	.	.	x
Sorex unguiculatus	Long-Clawed Shrew	10	0.9956	.	.	x
Desmana moschata	Russian Desman	325	2.5119	.	x	.
Talpa altaica	Siberian Mole	87	1.9395	.	.	x
Lepus americanus	Snowshoe Hare	1497	3.1752	x	.	.
Lepus capensis	Brown Hare	2158	3.3340	.	x	.
Lepus mandshuricus	Manchurian Hare	3330	3.5224	.	.	x
Lepus timidus	Blue Hare	2850	3.4548	.	x	x
Ochotona alpina	Northern Pika	120	2.0792	.	.	x
Castor canadensis	Beaver	23995	4.3801	x	.	.
Castor fiber	Beaver	13950	4.1446	.	x	.
Erethizon dorsatum	Porcupine	8505	3.9297	x	.	.
Dryomys nitedula	Forest Dormouse	27	1.4340	.	x	.
Eliomys quercinus	Garden Dormouse	92	1.9646	.	x	.

scientific name	common name	mass (g)	log mass (g)	NA	bm	Ebm	Rbm
Apodemus agrarius	Striped Field Mouse	21	1.3284	.		x	x
Apodemus flavicollis	Yellow-Necked Field Mouse	25	1.4041	.		x	.
Apodemus peninsulae	Korean Field Mouse	33	1.5172	.		.	x
Apodemus sylvaticus	Wood Mouse	23	1.3617	.		x	.
Arvicola terrestris	Ground Vole	238	2.3760	.		x	x
Clethrionomys gapperi	Gapper's Red-Backed Vole	27	1.4303	x		.	.
Clethrionomys glareolus	Bank Vole	22	1.3379	.		x	.
Clethrionomys rufocanus	Grey-Sided Vole	37	1.5682	.		x	x
Clethrionomys rutilus	Ruddy Vole	30	1.4771	.		x	x
Cricetus cricetus	Common Hamster	299	2.4762	.		x	.
Dicrostonyx torquatus	Arctic Lemming	95	1.9777	.		x	x
Eothenomys lemminus	Lemming sp	38	1.5798	.		.	x
Lemmus amurensis	Amur Lemming	92	1.9638	.		.	x
Lemmus lemmus	Norway Lemming	48	1.6767	.		x	.
Micromys minutus	Harvest Mouse	6	0.7559	.		x	x
Microtus agrestis	Short-Tailed Vole	30	1.4713	.		x	.
Microtus arvalis	Common Vole	25	1.4014	.		x	.
Microtus chrotorrhinus	Yellownose Vole	43	1.6286	x		.	.
Microtus fortis	Reed Vole	63	1.7993	.		.	x
Microtus gregalis	Narrow-Sculled Vole	48	1.6812	.		x	x
Microtus middendorffi	Middendorff's Vole	40	1.6067	.		.	x
Microtus oeconomus	Root Vole	19	1.2788	.		x	x
Microtus subarvalis	Vole sp	25	1.4014	.		x	.
Myopus schisticolor	Wood Lemming	29	1.4698	.		x	x
Ondatra zibethicus	Muskrat	1032	3.0136	.		x	x
Peromyscus maniculatus	Deer Mouse	23	1.3610	x		.	.
Synaptomys borealis	Northern Bog Lemming	33	1.5185	x		.	.
Synaptomys cooperi	Southern Bog Lemming	28	1.4518	x		.	.
Eutamias minimus	Least Chipmunk	44	1.6429	x		.	.
Glaucomys sabrinus	Northern Flying Squirrel	105	2.0208	x		.	.
Marmota camtschatica	Black-Capped Marmot	2010	3.3032	.		.	x
Marmota marmota	Alpine Marmot	2010	3.3032	.		x	.
Pteromys volans	Flying Squirrel	168	2.2240	.		x	x
Sciurus vulgaris	Red Squirrel	330	2.5187	.		x	x
Spermophilus major	Russet Souslik	136	2.1335	.		x	.
Spermophilus parryi	Arctic Souslik	745	2.8722	.		.	x
Tamias sibiricus	Siberian Chipmunk	96	1.9814	.		.	x
Tamiasciurus hudsonicus	Red Squirrel	191	2.2819	x		.	.
Napaeozapus insignis	Woodland Jumping Mouse	22	1.3512	x		.	.
Sicista betulina	Northern Birch Mouse	10	0.9890	.		x	x

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BIOGRAPHICAL SKETCH

Born in Murrayville, British Columbia, Canada, I was raised most of my life in Clearbrook, B.C. This beautiful rolling landscape of raspberry and dairy farms is enveloped by walls of mountains and a low ceiling of drizzle. As a boy, I would regularly run down to the neighborhood pond with my brother, a net, and a bucket. We were always fascinated with the bugs, tadpoles, and sticklebacks we'd catch. My real connection with the natural world though came from spending every summer in a cabin on the shore of Kootenay Lake in Southeast B.C. This mossy forest is on the edge of grizzly country. Observing everything around me while canoeing, hiking, and star-watching, I wondered how it all came to be.

Drawn to science, I tried to figure it all out by attending the University of B.C. There I studied everything from astronomy and geology to fine arts and poetry to computer science and mathematics. Although I found all fascinating, I had difficulty choosing. That is, until I met C.S. "Buzz" Holling while taking his biomathematics course. Buzz inspired me to take a holistic approach to science, one in which I could integrate across disciplines rather than pursue reductionist studies. Once I graduated with my double major in biology and ecology, I decided to take Buzz up on his offer and continue my studies with him down at the University of Florida.

Living in a different country is always an enlarging experience. I'd never seen so much sun, or such large reptiles and cockroaches. North Florida has many distractions: beaches, springs, prairies, and tourist towns.

The new friends I made opened my eyes greatly. The zoology department contains an extremely diverse group of people. The broad and deep conversations I had with scholars, preachers, warriors, and outcasts challenged my old explanations for the world and forced me to mature.

I had always set my sights on research, but had never considered teaching. It was my first year at UF where I took up teaching my first laboratories in core biology. I was quite surprised to learn that I was both good at it and that I very much enjoyed it. The students were so much fun to work with. I discovered that the enthusiasm I brought to the classroom was reflected back to me by the students; thus, making it a very positive experience. My enjoyment I was getting from the challenge of explaining things in a way that was clear and interesting to each student was outpacing the enjoyment I got from my research. My parents are both teachers and somehow they instilled an appreciation for it in me. My own experiences with poor teachers, particularly while at UBC, crystallized my resolve to do better with my students. I hope that I'll be able to continue teaching at a junior college or university.

With regards to the research, it was rather bewildering in the beginning. The work gained momentum once Buzz and I decided that I should work on fire in the boreal forest. The two trips I took up to Manitoba to gather data and do fieldwork were great. The boreal forest is beautiful and vast. One can't help but be taken aback both by the hum of activity in the summer and the deep, sublime winter. Once back in Florida, I began the tedious task of data entry and analysis. The great volume of data was one thing, but the problems with analysis were quite another. I could have applied the available methods and been done with it, but, that was not to be the case. I just had to be curious and careful with the work I was doing. In

doing so, I discovered, much to my chagrin, that there was no good way to measure the pattern I was looking for with the available methods. Thus began the long and arduous development of a statistical method for finding complex multimodality. I always thought that a simple solution was just around the corner. I am no doubt a plodder. I've discovered first hand that that's what research requires. Most of the time, I had no trouble being fascinated by the puzzles I was trying to solve. I must admit to a penchant for mathematical puzzles, especially those whose solution can have real utility. The tough part of graduate school, however, is the additive effects of repeated failure. I suppose that I have a real stubborn streak. I refused to resign to failure and so I just kept at it until I eventually stumbled upon a solution. Wrapping up the research came along quickly from that point. There can be little doubt, however, that I am a different person for the experience. I hope I'll be able to continue in my research at a college or university. At this point, I'm not sure whether I'd prefer a position that emphasizes teaching or research. The two together would be most rewarding.

I must also mention that during the course of this work, I had the privilege of working with Garry Peterson on a modeling project. My own background in computer modeling and biology meshed very well with Garry's specific expertise in modeling. We were able to investigate how fire/forest patterns and dynamics can emerge in intriguing variety with a series of simple spatial models. My fruitful collaboration with Garry helped guide my work on this dissertation. This experience also refined my own ability to utilize the unique capability of models to answer specific questions that can't be addressed through more traditional research approaches.

All being said and done, I am most grateful for the opportunities I have been given. Not only have I been able to pursue the life in research that I

have always aspired to, I have become a better person for it. It's the personal challenges that have made it all worthwhile.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Crawford S. Holling, Chair
Arthur R. Marshall, Jr., Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Carmine A. Lanciani
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Larry R. McEdward
Associate Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Colin A. Chapman
Assistant Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Henry L. Gholz
Professor of Forest Resources and Conservation

This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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Dean, Graduate School